

ESTIMATES OF SIZE AND INTERACTION
OF THE SOUTH AFRICAN ANCHOVY AND
PILCHARD POPULATIONS

by

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ABSTRACT

The size of the South African anchovy and pilchard population was estimated using Virtual Population Analysis (Gulland 1965). These estimates were used to test classical stock recruit models as well as to investigate possible stock interactions. The population biomass of the pilchard indicated a severe decline after 1959 from a level of approximately 2 000 000 metric tons to about 200 000 metric tons in the mid 1970's. This change was in agreement with catch per unit effort estimates of abundance (Newman et al in press). The anchovy abundance remained fairly constant at about 300 000 metric tons during the period 1965 - 1974 for which estimates could be made. During 1976 the pilchard stock showed a partial recovery of its former abundance. Adult and recruit stocks of both anchovy and pilchard were fitted to the Ricker (1954) and Beverton and Holt (1957) stock/recruit curves, but there was insufficient data to allow a decision to be made as to which model was appropriate for either stock.

The anchovy and pilchard populations or age groups within them do not appear to interact in a very definite manner. Attempts to quantify interactions using Virtual Population Analysis have not been successful although better estimates of the strength

of age-groups would be possible if the variation in natural mortality with age was understood.

The fact that elements of the stock of anchovy and pilchard do not appear to be rigorously related indicates the importance of understanding which environmental factors are critical to survival.

A difference between the area in which recruitment takes place and the area in which most adults are caught indicates a movement of young fish onto the west coast fishing grounds. The movements were substantiated by observations of catch per unit effort of juveniles on the west coast in each month of the fishing season.

II

FOREWORD

The method central to this thesis, Virtual Population Analysis, was developed elsewhere and is referenced in the appropriate section. The author is responsible for the application of the technique to South African fish species data. The FORTRAN programme for the manipulation of the standard equations was written by the author and carried out on a UNIVAC 1106 computer.

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INTRODUCTION

The Western Cape pelagic fishery.

South African catches of pelagic fish are centred in waters off the Western Cape. The fishery was established in 1943 but catch records are only reliable from 1950 onwards.

At least six species have contributed to the catch, these being the anchovy (Engraulis capensis), pilchard (Sardinops ocellata), maasbanker (Trachurus trachurus), mackerel (Scomber japonicus), red-eye (Etremeus teres) and lantern fish (Lampanyctodes hectoris). Catches made off the Western Cape are shown in table I.

Considerable changes in fishing power and catch composition have occurred since 1950 (Newman et al in press). The introduction of a 12,7 mm stretched mesh net during 1964/1965 to replace the 32 mm and 38 mm nets previously used led to the appearance in the catch of more small individuals and an increase in anchovy, red-eye and lantern fish landings. After 1964 the anchovy and pilchard together comprised well over half of the landings. The two species therefore formed the major component of the industry which produced canned fish, fish meal and oil.

Canned pilchard is more remunerative than the meal and oil which is mainly derived from the smaller specimens of all species. Added impetus is thus provided for studying the interactions between species, with a view to successfully managing the stocks.

Pilchard landings declined considerably after 1962. This phenomenon has been associated by several authors with competition from the anchovy. Stander and Le Roux (1968) suggest that as both species have a mixed diet including phyto- and zooplankton there is likely to be an equilibrium between the respective populations. This implies that food limits the abundance, a theory that has not yet been substantiated.

The existence of a natural balance between anchovy and pilchard populations has also been discussed by Murphy (1966). This author coupled the decline of the Pacific sardine (Sardinops caerulea) with high fishing effort and with increasing competition from the anchovy. The mechanism of this competition was thought to have been for food particles, or through anchovy preying on pilchard larvae. However, the increase in the anchovy population off California appeared after the decline in sardine landings,

suggesting that competition was mediated through the environment, in one or more steps. This could have happened if a reduced pilchard population allowed food available to the anchovy population to build up gradually.

TABLE I

COMPOSITION OF THE SOUTH AFRICAN PELAGIC CATCH

1950-1976 (thousands of metric tons)

YEAR	PILCHARD	ANCHOVY	MAAS-BANKER	MACKEREL	RED-EYE	LANTERN FISH	TOTAL
1950	85,3	-	49,9	-	-	-	135,2
1951	101,9	-	98,5	-	-	-	200,4
1952	170,0	-	102,6	-	-	-	272,6
1953	132,5	-	85,2	-	-	-	217,7
1954	88,3	-	118,1	4,0	-	-	210,5
1955	121,9	-	78,8	20,2	-	-	221,0
1956	76,6	-	45,8	32,6	-	-	154,9
1957	109,5	-	84,6	7,4	-	-	201,5
1958	194,4	0,2	56,4	21,6	0,8	-	273,4
1959	260,2	1,4	17,7	33,1	2,6	-	314,9
1960	318,0	-	62,9	31,0	0,1	-	412,0
1961	402,2	-	38,9	49,7	0,1	-	490,9
1962	410,2	-	66,7	20,4	0,1	-	497,3
1963	390,1	0,3	23,2	13,2	0,2	-	427,0
1964	256,1	92,4	24,3	50,0	2,7	-	425,6
1965	204,5	171,0	55,0	41,4	8,2	-	480,1
1966	118,0	143,9	26,3	53,4	15,4	-	357,1
1967	69,7	270,6	8,8	128,2	32,0	-	509,3
1968	107,8	138,1	1,4	91,0	30,3	0,1	368,6
1969	56,1	149,2	26,8	91,7	23,3	4,9	352,0
1970	61,8	169,3	7,9	77,9	23,7	18,2	358,9
1971	87,6	157,3	1,7	54,2	21,6	2,0	324,5
1972	104,2	235,6	1,3	56,7	20,6	15,2	433,6
1973	62,9	259,2	1,5	55,4	30,0	42,3	451,4
1974	16,8	348,6	2,4	31,2	1,2	0,3	400,5
1975	87,3	223,5	1,5	72,0	23,0	0,1	407,3
1976	175,6	219,4	0,4	0,5	11,5	0,1	407,5

Primary production.

Longhurst (1971) suggested some form of dynamic balance between the anchovy and pilchard populations and the plankton production in Cape waters, such that their combined biomass would equal that which could be supported by the planktonic food chain. Possible interspecific competition for food between anchovy and pilchard throughout their life cycles has been shown by King and MacLeod (1976). These authors also noted that both species were initially zooplanktophagous but became phytoplanktophagous at a standard length of 80 mm in the case of anchovy and at 100 mm in the case of pilchards. On the other hand Cushing (1969) estimated far greater total carbon fixation for the Benguela current system than for either the California current or the Peru/Chile upwelling area. Using different upwelling centres and rates of movement in the water column Andrews et al (1970) came to a similar estimate of carbon fixation. This suggests that food may not be a limiting factor. However, feeding at the larval stage is not well understood and it is possible that food quality and patchiness of the particles may be more critical to pilchard than anchovy. The anchovy egg has been noted as

more robust and more suited to high plankton densities than that of the pilchard. (Anders, Sea Fisheries Branch, pers. comm.)

Fecundity of pelagic fish appears to be more than sufficient to account for numbers of juvenile fish (MacGregor 1968) so that larval mortality, especially at the yolk sac absorption stage when feeding first takes place may be a dominating feature in year class survival.

Stock Assessments.

The study of interaction and management of the stocks requires annual estimates of stock size. Methods of assessment used in South Africa and South West Africa include parent stock egg-production relationships, aerial and acoustic surveys, analysis of catch and fishing effort, stock-production models, and yield per recruit estimates.

The parent-stock egg-production method (Nikolsky 1969) necessitates delineating the spawning grounds as well as the development of reliable egg-capture techniques, plus the establishment of the fecundity of the females from which index the spawning biomass

may be calculated. In addition, variation in sex ratios has to be taken into account in order to calculate the total biomass of both sexes.

Aerial-acoustic survey methods have many inherent problems (Cram and Hampton 1976). These include the difficulty of accurately delineating the fish-shoal from the rapidly moving aircraft, as well as the fact that acoustic target strength measurements are complicated by variation in density of the shoal in all dimensions, thus making representative sampling almost impossible. The advantage of aerial estimation of the stock is the speed with which stock size can be judged. However, several of the problems outlined above have yet to be satisfactorily resolved.

Catch and effort assessments (Newman et al in press) assume that availability remains constant, a dubious premise for fish species whose migrational habits are not well understood. Should the availability or catchability coefficient (q) vary unpredictably from year to year then units of fishing effort would not be comparable over these periods, and would not be useful in the formation of abundance indices such as catch per unit effort (c.p.u.e.)

Stock production models (Pella and Tomlinson 1969, Ricker 1975) postulate that a fish stock produces its greatest harvestable surplus when below maximum abundance. The level of effort which will maintain this surplus can be calculated. However, q is again an important parameter and is often erroneously assumed to be constant.

If natural mortality is variable, the concept of sustainable yield is not a safe one, since fishing effort at a particular level might in periods of high mortality be responsible for serious damage to stock. Generally natural mortality is assumed to be constant, an unlikely situation in a life cycle subject to the instabilities of the pelagic environment.

The yield per recruit model sums the yields contributed by all ages of a given year-class to obtain the total yield. The method requires information on fishing mortality inflicted on each age group and to obtain an equilibrium yield the number of fish at recruitment must also be known (Ricker 1975). The method is generally applied using a constant natural mortality rate with the drawbacks mentioned above.

Until year-class strength can be measured in advance and the size of the recruited population predicted so that quotas can be appropriately adjusted, the fishery will have to accept either wide variation in yield plus the risk of serious damage to the stock, or a smaller more stable yield based on conservative quotas.

The Management of Fish Stocks.

One of the aims of management is to develop the ability to predict strong and weak year-classes of each species in the fishery and thus enable fishing effort to be distributed in such a way as to maintain a favourable balance in the various fish populations. In order to do this effectively a knowledge of processes governing recruitment and stock size is necessary. These include fecundity, natural and fishing mortality in the population, availability of the population, and population interactions.

The objectives of this study were:

- (1) to estimate the South African anchovy and pilchard population biomasses by virtual population analysis (Gulland 1965)
- (2) to investigate whether the number of anchovy and pilchard recruits each

- year could be understood in terms
of both parent stock biomasses
(3) to investigate the dependence of
anchovy and pilchard abundance on
each other.

Virtual population analysis (V.P.A.) is described using standard equations and developed to test the effect of varying natural mortality rates during the lifespan of the fish on stock biomass estimates. The abundance of each age group provided by V.P.A. was used to test stock/recruit relationships and interactions.

Possible annual migrations of the anchovy and pilchard populations are mentioned with reference to V.P.A. and stock interactions.

DATA

Sampling procedure.

Purse seine vessels land fish at several ports around the Cape coast. The landings were recorded by factories at which canning and meal production took place. Daily samples comprised a bucket of fish taken from the hold of a boat whose catch was typical of the fleet landing at that harbour. From these samples the species and the length compositions were determined and 25 fish were removed for age determination by personnel of the Sea Fisheries Branch.

The sampling of the catch took place simultaneously at geographically separated harbours and thus length and species compositions were expected to differ. In order to reconcile catches to the sample most representative of them and thus obtain meaningful age compositions, the landings in each week were separated by locality and according to the species dominant at that landing. The catch weight of each species was obtained by splitting the tonnage (recorded by skipper and factory) for each area in each week by the species composition of the samples taken closest to that area-week.

The length composition of the samples taken closest to this landing in time and space was also associated with the catch, the result was numbers of fish in the catch per length group.

Catches in which more than one species occurred were called 'mixed', while single species catches were labelled 'pure'. The weight of the modal length group of the catch in each area-week was used to decide whether the majority of fish in that group were more than 50 per cent mature (and therefore adult) or immature and juvenile. Numbers of fish were obtained for adult and juvenile catches in order to examine possible differences in distribution. These operations were carried out by members of the Electronic Data Processing unit at the Sea Fisheries Branch.

Preparation of the Data.

The numbers of anchovy and pilchard caught in each age group were obtained for virtual population analysis (V.P.A.) using age-length keys established for the South African anchovy by Pollock (1970) and for the South African pilchard by Baird (1970). Subsequent to 1971 an age-length key established for each year was used for pilchard.

Equations representing these age-length relationships are listed below :

(a) Anchovy

$$L_t = 14,75 (1 - e^{-0,45(t+0,717)}) \quad (1)$$

where L_t is the caudal length at age t in cms

$$L_n = 1,1174 L_t + 0,6017 \quad (2)$$

where L_n is the total length at age t in cms

and

$$W_n = 0,00338 L_n^{3,25} \quad (3)$$

where W_n is the weight at age t in grs

Pollock (1970)

(b) Pilchard

$$L_t = 30,60 (1 - e^{-0,2247(t+1,505)}) \quad (4)$$

where L_t is the total length at age t in cms

$$L_n = 0,8357 L_t + 0,097 \quad (5)$$

where L_n is the caudal length at age t in cms

and

$$W_n = 0,00957 L_n^{3,0752} \quad (6)$$

Baird (1970)

The fishing season extends from January 1st to August 31st in most years, (this has been subject to changes on several occasions) and both anchovy and pilchard spawn from September at least through February so that catches of each age group may be assumed on average to be half way toward their next birthday. Length at age was therefore calculated at $t = 0,5; 1,5; 2,5$ and so on representing the ages 0, 1, 2, etc. Similarly therefore W_n represents the weight calculated for fish midway between age groups. The numbers of anchovy and pilchard calculated in each age group in the catch are shown in tables II and III.

Parameter Estimates.

The importance of the natural mortality rate assumptions for V.P.A. has been mentioned. Growth and mortality of the South African anchovy were studied by Pollock (1970). The number of fish caught in each age group during 1964 when fishing mortality can be assumed to have been low, was used to calculate natural mortality (M). This was possible because the 12,7 mm net, the only gear which captured anchovy effectively, was only partially introduced and the rate at which the number of fish decreased in the fully selected age groups could be equated with M .

An instantaneous M value of 0,8 was thus obtained.

Tagging experiments (Newman 1970) suggested a maximum natural mortality of 0,6 for the pilchard, and this value was therefore selected as an upper limit. An M value of 0,5 was used as a conservative estimate in calculations.

The sensitivity of the estimates to variations around these values of M was examined and will be discussed in the following section.

An estimate of the terminal fishing mortality (F_t) for each year-class is also necessary for V.P.A. calculations. F_t reflects the mortality caused by fishing on the oldest fish in every year-class. These are, for example, the four-year-olds in the case of anchovy (Table II).

F_t can be obtained from the exploitation rate (u) defined as :

$$u = \frac{F(1 - e^{-Z})}{Z} \quad (7)$$

Ricker (1975)

where Z is the total mortality.

Equation (7) expresses the proportion of the total deaths which are due to fishing.

The survival rate (e^{-Z}) becomes negligible for fish near the end of their life span, so that the actual mortality rate ($1 - e^{-Z}$) approaches 1.

Thus u becomes

$$u = \frac{F}{Z} \quad (8)$$

The value of equation (8) depends upon the change of F relative to M . Where M is assumed to be constant and Z increases with age, u tends toward 1. In practice, u is often taken as being close to 1 and F_t calculated from (8).

A second way of estimating F_t has been attempted; the hypothesis is put forward that fully selected age groups in fish populations have F values that tend toward an asymptote with increasing age.

F_t is therefore chosen to minimize the difference between the assumed value of F_t and the fishing mortality in the year class during the previous year. During the period 1967-1970, fishing effort remained relatively stable, and therefore this period was used in the calculation. Trials with a series of F_t values indicated that an exploitation rate (u) close to 0,7 was appropriate for both anchovy and pilchard populations using this method. This method was adopted because the u result was not very different from the u assumption considered earlier.

The sensitivity of the population estimates to variations of F_t was examined and will be discussed in the following section.

In some year-classes older fish are not represented among the catches, and it is necessary to estimate F_t for younger age groups. In these cases it is less realistic to assume a high rate of exploitation and F_t was estimated using the average of the same age group over several earlier years. This method was suitable for the anchovy population where availability and fishing effort were reasonably constant over the period used to estimate the average.

In the case of the pilchard, however, the availability of the population appeared to change substantially during 1974-1976. F_t values were therefore assumed to be equal to those of 1965 when a catch per unit effort, and presumably abundance, similar to that for 1976 was recorded for all species and the catch of pilchard was of the same order as that in 1965. If there is a period when effort directed toward a species remains stable, average F values during this period may be used to estimate F_t values in the current year by adjusting F to take account of changes in effort (Newman et al 1976).

TABLE II

NUMBER OF ANCHOVY CAUGHT (IN MILLIONS) PER AGE CLASS

YEAR	0	1	2	3	4
1964	4 113	3 692	1 032	265	26
1965	6 113	5 888	2 552	847	107
1966	17 472	3 755	876	263	24
1967	31 844	8 111	1 300	518	104
1968	13 353	4 810	702	227	42
1969	18 344	4 314	612	158	20
1970	24 598	4 523	830	209	27
1971	12 823	5 464	1 192	485	70
1972	10 108	7 417	1 619	656	121
1973	24 988	5 932	538	53	-
1974	19 260	12 501	1 990	322	9
1975	26 390	5 657	1 500	302	11
1976	18 336	7 639	1 085	193	17

TABLE III

NUMBER OF PILCHARD CAUGHT (IN MILLIONS) PER AGE CLASS

YEAR	0	1	2	3	4	5	6	7	8
1950			4	64	176	222	146	24	1
1951			5	44	210	280	169	27	1
1952	1	4	20	224	475	436	206	23	1
1953		4	27	87	337	391	175	19	
1954				21	204	281	132	9	
1955				22	261	403	187	12	
1956		4	9	45	140	225	134	11	
1957		3	63	174	290	271	123	18	
1958			113	1 071	651	208	59	6	
1959	2	27	413	1 719	927	156	9		
1960	1	15	323	1 714	1 300	291	17		
1961		2	77	827	1 903	847	102	1	
1962		1	163	1 305	1 651	768	140		
1963	16	178	839	1 234	1 528	682	93	1	
1964	1	13	252	1 081	918	264	21		
1965	235	129	318	1 027	599	156	15		
1966	370	74	55	405	412	151	17		
1967	3 623	813	108	156	56	7			
1968	4 307	643	159	354	198	44	3		
1969	2 558	326	204	255	54	7			
1970	1 632	421	193	357	60	3			
1971	4 489	682	164	297	88	8			
1972	1 317	687	204	202	216	77	13		
1973	2 244	13	180	190	27	1			
1974	0	47	17	51	56	20	4		
1975	2 432	433	186	188	104	36	1		
1976	19	435	1 225	738	124	12			

VIRTUAL POPULATION ANALYSIS

Method and Standard Equations.

The equations developed form a summary of existing techniques. The use of the term virtual population analysis has been ambiguous in the literature, because the analysis has been modified since its introduction.

A virtual population was defined by Fry (1949) as "the sum of the fish belonging to a given year-class present in the water at any given time, that are destined to be captured in the fishery in that and all subsequent years". This sum of catches from a particular year-class is a minimum estimate of its abundance at that time and has also been referred to as the utilized stock. (Ricker 1975) Some workers have used the catch of an age group plus Fry's virtual population as defined to estimate u . This gives a rate which is higher than the true rate of exploitation because the virtual population underestimates the true population. Hence :

$$\frac{x^C_n}{x^V_n} = u \quad (\text{max}) \quad (9)$$

where x^C_n is the catch of age n in year-class x and x^V_n is the virtual population of age n in year-class x .

The true value of u is calculated as the proportion of the cohort caught in any year. This is smaller than u (max) as the number of fish caught subsequently from a year-class x^V_n must always be less than the total number in the class, so that :

$$u = \frac{x^C_n}{x^N_n} < \frac{x^C_n}{x^V_n} \quad (10)$$

where $x^N_n = x^V_n + \text{the fish destined to die naturally}$

The number of fish caught can be expressed as the proportion of deaths in the population caused by fishing.

$$x^C_n = \frac{x^F_n (1 - e^{-x^Z_n}) x^N_n}{x^Z_n} \quad (11)$$

Beverton and Holt (1957)

where x^F_n = the fishing mortality of fish of age n in year-class x
and x^Z_n = the total mortality of fish of age n in year-class x

or rearranging

$$x^N_n = \frac{x^Z_n \cdot x^C_n}{x^F_n (1 - e^{-x^Z_n})} \quad (12)$$

Further, the number of fish in year-class x remaining in the population at the end of year n can be found from its original size and the total mortality :

$$x_{n+1}^N = x_n^N (e^{-x_n^Z}) \quad (13)$$

Gulland (1965) argued that the fishing mortality in any year could be calculated from the ratio of (12) and (13) as

$$\frac{x_n^C}{x_{n+1}^N} = \frac{x_n^F (1 - e^{-x_n^Z})}{x_n^Z \cdot e^{-x_n^Z}} \quad (14)$$

Equation (14) can be solved by iteration. The equations (12) and (14) are used successively until the cohort size of each age of every year has been obtained.

For example the 1966 year-class of the South African pilchard may be summarized as :

Year	1966	1967	1968	1969	1970	1971	1972	1973
Age	0	1	2	3	4	5	6	7
Number of fish caught ($\times 10^6$)	370	813	159	255	60	8	13	0

Assuming an exploitation rate of 0,72 (see results) and a natural mortality of 0,5, F_t is calculated as 1,28 (equation 8). Using equation (12), the number of six year old fish in the population is equal to :

$$1966N_6 = \frac{1,78 \cdot 13}{1,28 \cdot (1 - e^{-1,78})} = 22$$

Now equation (14) becomes

$$\frac{8}{22} = \frac{F \cdot (1 - e^{-(F+0,5)})}{(F+0,5) \cdot e^{-(F+0,5)}}$$

The value of F is thus 0,256. The number of five year olds in the population can then be estimated using the calculated value of F in equation (14).

It is not possible to estimate fishing mortality using equation (14) for age groups which are not represented in the samples and it is assumed that all deaths occurring at this age in the year-class were natural so that :

$$x_n^N = x_{(n+1)}^N \cdot e^{+M} \quad (15)$$

Virtual population analysis (V.P.A.) has been adapted for simple solution in populations having low natural mortality by Pope (1971). Pope called his method cohort analysis. In general, cohort analysis is applicable to populations with a natural

mortality not exceeding 0,2. The South African pelagic fish populations that are dealt with here are believed to have natural mortalities higher than 0,2 (Newman 1970, Pollock 1970) so that Pope's method will not be discussed.

Results and Sensitivity Tests.

The F values calculated (from equation 14) and the F_t value assumed are recorded for the anchovy and pilchard populations in Tables IV and V.

The sensitivity of estimates to the value of F_t on the population result depends upon the degree of fishing mortality accumulated by the year-class. For constant values of M , the higher the accumulated fishing mortality the less effect of an erroneous F_t value on the population estimate. The population estimate of a species for which many age groups appear in the catch is therefore likely to be less sensitive to F_t assumptions than one whose appearance in the catch is of short duration. This is demonstrated for the anchovy and for the pilchard populations in Tables VI and VII. The differences in the population sizes for both populations are shown to be generally less than 10 per cent over the range of u values considered.

TABLE IV

CALCULATED FISHING MORTALITY SOUTH AFRICAN ANCHOVY
(NATURAL MORTALITY = 0,8).

YEAR	0	1	AGE 2	3	4
1964	0,164	0,384	0,454	0,715	2,047
1965	0,306	0,790	1,160	2,661	2,047
1966	0,566	0,651	0,519	0,723	2,047
1967	1,015	1,380	1,156	1,785	2,047
1968	0,475	0,905	0,890	1,710	2,047
1969	0,617	0,569	0,555	1,223	2,047
1970	0,795	0,631	0,404	0,810	2,047
1971	0,463	0,908	0,720	0,979	2,047
1972	0,333	1,275	2,330	> 9	2,047
1973	0,529	0,701	0,570	1,245	2,047
1974	0,669	1,345	1,310	2,515	2,047
1975	0,692	0,945	1,406	2,093	2,047
1976	0,630	0,997	1,095	1,951	2,047

TABLE V

CALCULATED FISHING MORTALITY SOUTH AFRICAN PILCHARD
(NATURAL MORTALITY = 0,5).

YEAR	AGE								
	0	1	2	3	4	5	6	7	8
1950				0,028	0,155	0,517			
1951				0,018	0,164	0,563	0,680		
1952			0,005	0,099	0,383	0,900	2,030	3,051	1,279
1953			0,010	0,041	0,296	0,965	2,481	3,474	1,279
1954				0,013	0,176	0,631	2,036	2,834	1,279
1955				0,019	0,313	0,937	2,386	3,467	1,279
1956				0,043	0,220	0,719	1,755	3,477	1,279
1957			0,010	0,109	0,614	1,388	2,291	4,805	1,279
1958			0,010	0,337	1,146	2,683	4,559	1,279	1,279
1959		0,002	0,035	0,302	0,823	1,770	2,739	1,279	
1960		0,001	0,037	0,276	0,571	1,063	1,877	1,279	
1961			0,011	0,172	0,838	1,588	4,766	1,279	
1962			0,031	0,345	0,916	1,841	4,346	1,279	
1963	0,005	0,036	0,195	0,486	1,430	3,041	4,511	1,279	
1964		0,006	0,089	0,599	1,353	2,149	4,231	1,279	
1965	0,096	0,089	0,283	0,924	1,305	1,588	1,279	1,279	
1966	0,095	0,054	0,068	1,096	2,847	6,184	1,249		
1967	0,573	0,437	0,144	0,389	0,626	0,672	1,279		
1968	0,723	0,260	0,196	1,544	2,508	4,864	1,279		
1969	0,701	0,146	0,169	0,821	2,287	1,279	1,279		
1970	0,398	0,329	0,166	0,736	0,688	1,999			
1971	0,952	0,411	0,289	0,597	0,587	0,256	1,279		
1972	0,478	0,525	0,290	1,068	2,507	6,377	1,279		
1973	0,319	0,011	0,357	0,712	0,556	0,116	1,279		
1974	0 ?	0,013	0,023	0,225	0,698	1,964	1,279		
1975	0,252	0,052	0,091	0,524	1,620	3,770	1,279		
1976	0,096	0,089	0,283	0,924	1,305	1,588	1,279		

TABLE VI

CALCULATED ANCHOVY BIOMASS FOR VARIOUS FINAL
EXPLOITATION RATES (U) metric tons ($\times 10^3$)
(NATURAL MORTALITY = 0,8)

YEAR	U		
	0,5	0,7	0,9
1964	328	306	297
1965	325	306	298
1966	303	289	283
1967	358	343	338
1968	265	246	238
1969	307	287	280
1970	341	326	321
1971	305	295	291
1972	297	290	288
1973	375	370	368
1974	389	384	382
1975	337	332	330
1976	314	309	307

TABLE VII

CALCULATED PILCHARD BIOMASS FOR VARIOUS FINAL
EXPLOITATION RATES (U) metric tons ($\times 10^3$)
(NATURAL MORTALITY = 0,5)

YEAR	U		
	0,5	0,7	0,9
1950	913	910	910
1951	931	926	924
1952	867	860	856
1953	720	712	708
1954	645	637	635
1955	744	736	733
1956	1 050	1 040	1 040
1957	1 520	1 520	1 510
1958	1 890	1 890	1 890
1959	2 070	2 040	2 040
1960	1 980	1 940	1 940
1961	1 730	1 700	1 700
1962	1 390	1 370	1 360
1963	1 010	989	981
1964	613	598	592
1965	394	382	378
1966	254	243	239
1967	268	259	255
1968	297	286	282
1969	251	241	238
1970	243	235	232
1971	260	254	251
1972	194	189	187
1973	205	203	202
1974	351	350	349
1975	551	550	550
1976	529	529	529

Pope (1971) showed that for a cumulative F of 2,0 for a stock with a natural mortality of 0,2 overestimating the terminal fishing mortality (F_t) by 100 per cent gave an error in the population of almost -7 per cent and an error in other F values of +7 per cent. On the other hand, underestimating F_t by 50 per cent under the same conditions led to a percentage error in the population of +14 per cent and an error of -12 per cent in other F values. The bias in F caused by incorrect choice of F_t was greatest amongst older age groups.

Anchovy and pilchard population sizes were calculated using constant M values of 0,8 and 0,5 respectively. The number of fish in the population (calculated from equation 12) are shown in Tables VIII and IX for anchovy and pilchard stocks respectively. Total population biomass estimates are given for the respective populations in Tables X and XI.

The anchovy population showed little trend over the years considered, the biomass remaining in the region of 350 000 metric tons, with a peak in 1974 of 384 000 metric tons. The pilchard increased greatly from less than one million metric tons to

over two million in 1959. This biomass, which was largely made up of young fish preceded the record catches in 1962 of over 400 000 metric tons.

Unfortunately regular landings of anchovy were not made before 1964, thus one cannot compare biomass estimates of the two populations during an important phase when pilchard abundance was at a peak.

Total biomass estimates of the maasbanker (horse mackerel), mackerel and red-eye species are included in appendix 3. Unfortunately the data series for these species is incomplete. The maasbanker occur irregularly in the pelagic landings, and were caught only in small quantities after 1962 making the data unfit for V.P.A. The mackerel were not sampled for length frequency prior to 1964 so that age distributions and V.P.A. estimates cannot be made. Red-eye were landed in small amounts before 1964 and were also not sampled for length frequency.

Studies on the error introduced in V.P.A. due to uncertainties in the natural mortality and sampling error in the catch has been carried out by Agger et al (1971) and by Pope (1971). The errors were directly calculated by choosing different values of M , though M was always assumed

constant within the year-class. A similar sensitivity analysis was conducted on the South African hake (Merluccius capensis) results of which are contained in a publication included as appendix 1. Likely limits to the natural mortality of anchovy and pilchard are also tested and presented in Tables X and XI.

These results showed that an increase from $M = 0,8$ to $M = 0,9$ (12,5 per cent in natural mortality rate) on the anchovy population led to a similar increase in the biomass estimate. The increase was consistent over all years, suggesting an unchanging rate of exploitation in the fishery (see Table X). On the other hand an increase of 20 per cent in the natural mortality rate of the pilchard (from $M = 0,5$ to $M = 0,6$) led to increases in the biomass estimates of between 15,4 per cent in 1971 when the weighted fishing mortality (\bar{F}) was at a maximum of 0,78 to 40,4 per cent in 1956 when \bar{F} was at a minimum of 0,02 (see Table XI).

The operation of a fishing season has been mentioned. This could affect V.P.A. estimates as the Beverton and Holt catch equation (12) is based on evenly distributed fishing and natural mortality throughout the year. However, Ulltang (1976) has shown that the degree of error involved in V.P.A.

when fishing effort is restricted to a particular fishing season is generally negligible.

TABLE VIII

CALCULATED ANCHOVY NUMBERS IN THE POPULATION
(IN MILLIONS) (NATURAL MORTALITY = 0,8)

YEAR	AGE				
	0	1	2	3	4
1964	39 100	16 400	3 990	719	38
1965	33 000	14 900	5 020	1 140	158
1966	56 600	10 900	3 040	707	36
1967	68 000	14 400	2 560	812	154
1968	49 800	11 100	1 630	362	61
1969	55 600	13 900	2 010	301	29
1970	61 900	13 500	3 540	519	40
1971	48 800	12 600	3 220	1 060	104
1972	50 800	13 800	2 270	704	179
1973	85 300	16 400	1 730	99	-
1974	55 000	22 600	3 650	441	13
1975	73 400	12 700	2 640	442	16
1976	54 700	16 500	2 210	291	25

TABLE XI

CALCULATED BIOMASS OF PILCHARD AT DIFFERENT VALUES
OF NATURAL MORTALITY ($U = 0,7$) (metric tons $\times 10^3$)

YEAR	0,4	^M 0,5	0,6
1950	633	910	1 280
1951	696	926	1 260
1952	663	860	1 140
1953	551	712	941
1954	494	637	841
1955	560	736	994
1956	760	1 040	1 460
1957	1 120	1 520	2 110
1958	1 440	1 890	2 550
1959	1 600	2 040	2 660
1960	1 560	1 940	2 430
1961	1 410	1 700	2 080
1962	1 170	1 370	1 640
1963	861	989	1 150
1964	525	598	690
1965	340	382	436
1966	210	243	286
1967	220	259	310
1968	245	286	343
1969	203	241	292
1970	200	235	280
1971	223	254	293
1972	163	189	224
1973	164	203	254
1974	282	350	435
1975	485	550	626
1976	507	529	552

Variable Natural Mortality Trial.

In the literature natural mortality is considered to be constant throughout the life history of fish. However, Deevey (1947) examined the trend of natural mortality with age for a variety of animals. Common to all was a downward trend in mortality during the juvenile to sexual maturity stages. Equally there was generally an upward trend in mortality amongst older animals. Density dependent natural mortality has also been suggested for some species by Cushing (1975) and others. In addition, increasing mortality beyond a critical age has also been suggested, Greer-Walker (1970).

It is improbable, therefore, that natural mortality is constant throughout the life of anchovy and pilchard, and an attempt has been made here to develop the V.P.A. technique to include a variable M value.

An intuitive series of M values for each age group along the lines mentioned above were tested. Actual values chosen are shown on Table XII. The mean M was held constant at 0,5 while M values for young and old fish were raised and M values for fish in the middle age groups were lowered, using the South African pilchard as an example. The results were

recorded as the percentage change in the population biomass for the periods 1959/1962 when fishing effort was reasonably stable at a low level and for the period 1968/1971 when effort was stable at a higher level (Table XIII). The modified values represent an increase of up to 80 per cent on the youngest and oldest groups and a decrease of up to 60 per cent on middle aged groups.

The result of varying M depends on the age groups dominant in the catch relative to the virtual population of their respective year-classes.

Table XIII shows that trials 1-3 (Table XII) resulted in a greater change during 1959/1962 than 1968/1971. The preponderance of middle aged fish in the catches during the earlier period accounts for this result.

During 1968/1971 fish less than one year old predominated in the catches (Table II) nevertheless all trials led to a reduction in biomass. This reflects the smaller contribution of recruit biomass to the total. The intuitive series of M values reduces the order of the apparent decline in pilchard abundance.

TABLE XII

NATURAL MORTALITY VALUES ASSUMED AT EACH AGE GROUP
IN TRIAL V.P.A. OF SOUTH AFRICAN PILCHARD

TRIAL	0	1	2	AGE 3	4	5	6	7
1	0,7	0,5	0,4	0,4	0,4	0,4	0,5	0,7
2	0,8	0,6	0,3	0,3	0,3	0,3	0,6	0,8
3	0,9	0,7	0,2	0,2	0,2	0,2	0,7	0,9

TABLE XIII

CALCULATED PILCHARD BIOMASS USING VARIABLE NATURAL
MORTALITY (metric tons $\times 10^3$) AND PERCENTAGE CHANGE
COMPARED WITH CONSTANT VALUE

TRIAL	1959/1962		1968/1971	
	AVERAGE BIOMASS	% CHANGE	AVERAGE BIOMASS	% CHANGE
1	1 518	-13,9	238	-6,1
2	1 338	-24,1	230	-9,5
3	1 198	-32,1	224	-11,7
CONSTANT	1 763	-	254	-

Agger et al (1971) also examined the effect of standard deviation in catches. The result was approximately half the equivalent standard deviation of fishing mortality. Similarly the variance in the population with respect to that of the catches depends upon the fishing mortality per year and the number of years of exploitation. The greater the exploited life of the species the less sensitive the population result would be to variance in the catches.

RECRUITMENT

Method and mechanisms.

Recruitment is the process in which young fish enter the exploited area and become liable to contact with the fishing gear (Gulland 1965). The definition emphasizes the part played by the behaviour of the fish, shoaling, migrations and distribution, all making the species more or less liable to capture. By contrast the nature of the gear governs the size of fish captured and is referred to as selectivity. Locational devices allowing fish to be detected and caught by both day and night also change the pattern of selectivity.

The process of selection is usually gradual, with an increase in vulnerability of members of a year-class over a period of two or more years. This is known as continuous selection. However, the event may take place over a shorter period, approaching the theoretical knife-edge type recruitment, whereby fish at a given age become vulnerable at a particular time in a given year and remain equally vulnerable.

In 1965 the full scale introduction of a new purse-seine net changed the pattern of recruitment in the South African pilchard fishery to one more like the knife-edged kind, because the largest number of fish

in the catches of both anchovy and pilchard are often not yet one year old. Juvenile fish move into the fishing grounds and are liable to contact with the fishing gear at a given age, as described in the section on migration.

The two most commonly considered descriptions of the stock/recruitment relationship are :

$$(1) \quad R = aPe^{-bP}$$

where R = number of recruits

P = size of parental stock (16)

and a & b are constants Ricker (1975)

$$(2) \quad R = \frac{P}{PW + K} \quad (17)$$

where W and K are constants

Beverton and Holt (1957)

Both relationships endeavour to describe the replacement of a parental population, but under different biological situations. The Ricker model is more appropriate when cannibalism of young by adults is an important regulatory mechanism or when density inhibits growth through a crucial phase, or

when there is a time lag in the response of a predator to the abundance of young fish it consumes. This can be understood from the form of the curve (Fig. 1) showing the theoretical stock/recruit relationship. The initial steep rise is suitable for a period of unhindered increase in recruitment proportional in a direct manner to the population size. Subsequently the recruits are assumed to be subject to an exponentially increasing depressant effect when the crucial phase or time lag has elapsed.

Lett and Kohler (1976) working with Gulf of St. Lawrence herring statistics confirmed Ricker's (1954) suggestion that density dependent mortality is generated by the aggregation of predators upon the fish larvae, and hence the more larvae the more predation.

The Beverton and Holt model describes the stock/recruit relationship when food or habitat is a limiting condition or when predation adjusts quickly to the amount of prey. (Ricker 1975). The form of the equation includes a constant (K) which is related to the carrying capacity of the environment. The curve which uses the South

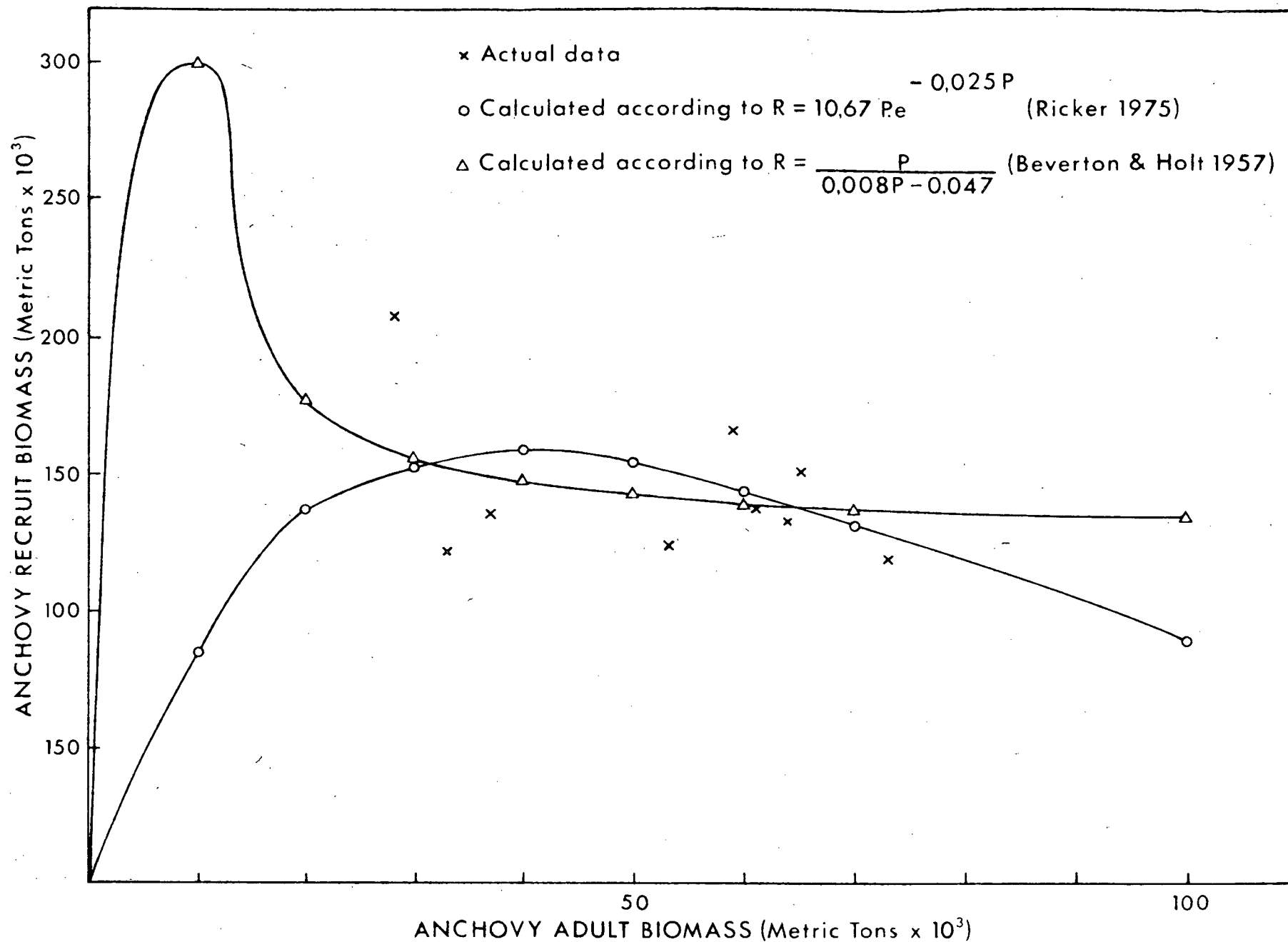


FIG.1. ANCHOVY STOCK / RECRUIT CURVE

African pilchard as an example (Fig. 2) shows how recruits are expected to change with population size using this model.

Results.

Data on the biomass of recruit and adult stock of anchovy and pilchard were fitted to both Ricker and Beverton and Holt models (equations 16 and 17) using the method of least squares. Data and results are shown on Tables XIV and XV for the anchovy and pilchard populations respectively. Fully mature anchovy were assumed to be all those fish two years of age and older and fully mature pilchard as four years of age and older.

Adult anchovy were considered as responsible for recruits in the same calendar year.

Equation (16) gave $r = 0,910$ ($P < 0,01$; 7 degrees
of freedom)

Equation (17) gave $r = 0,929$ ($P < 0,01$; 7 degrees
of freedom)

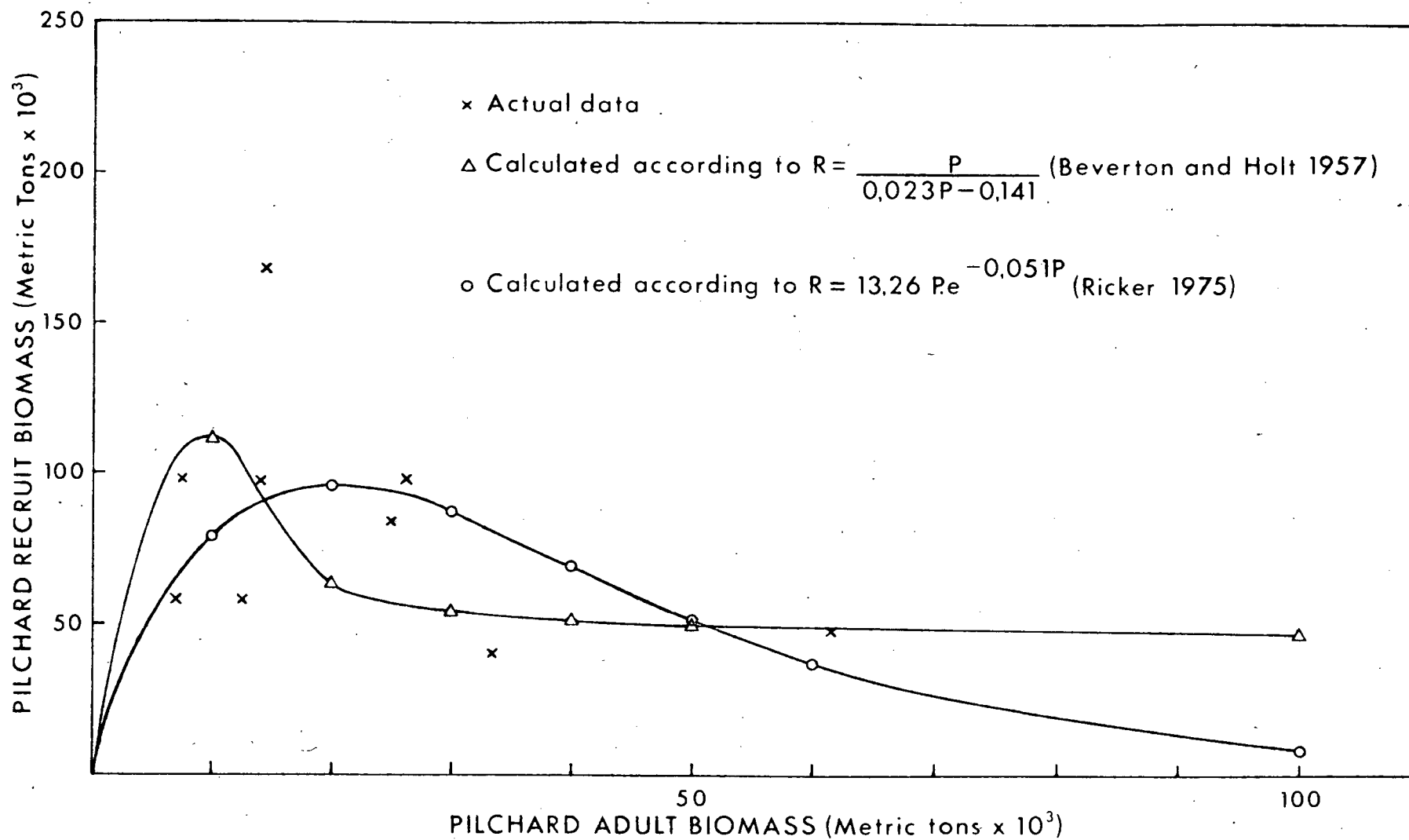


FIG. 2. PILCHARD STOCK RECRUIT CURVE.

TABLE XIV

CALCULATED ADULT ANCHOVY STOCK (TWO YEARS AND
OLDER) AND RECRUITS (0 YEARS OLD)

YEARS	ADULTS m.tons x 10 ³	RECRUITS m.tons x 10 ³
1966	61	137
1967	59	165
1968	33	121
1969	37	135
1970	65	150
1971	73	118
1972	53	123
1973	28	207
1974	64	133

Both models fit the observations at the one per cent level of significance, the probable reason for this being the flexible response of recruitment to parent stock size in the range covered by the data. The spread of data points and the theoretical curves generated by the two models are shown in Fig. 1.

Fig. 1 shows that two very differently shaped curves are generated by the models, pointing to the equivocal nature of the data and indicating that neither model can be selected as descriptive of the anchovy stock/recruit relationship. It is interesting to note, however, that equation (17) gave a slightly better fit to the data, and if it were more applicable that an increase in recruitment with reduced adult stock size would be expected.

TABLE XV

CALCULATED ADULT PILCHARD STOCK (FOUR YEARS AND
OLDER) AND RECRUITS (0 YEARS OLD)

YEARS	ADULTS m.tons x 10 ³	RECRUITS m.tons x 10 ³
1966	61,6	48,6
1967	14,2	96,5
1968	26,2	96,5
1969	7,0	58,6
1970	12,7	58,1
1971	25,0	83,6
1972	33,6	40,4
1973	7,8	96,5
1974	14,9	167,0

The pilchard biomass data was also fitted to
equations (16) and (17)

(16) gave $r_s = 0,897$ and ($P < 0,01$; 7 degrees
of freedom)

(17) gave $r = 0,946$ and ($P < 0,01$; 7 degrees
of freedom)

Fig. 2 shows the form of the Ricker curve, equation (16), and Beverton and Holt curve, equation (17), when the South African pilchard data (Table XV) is fitted to them by a least squares procedure. Although (17) had a higher correlation coefficient (r), it would not be statistically correct to infer that (17) showed a significantly better fit.

In conclusion it can be said of the stock/recruit curves that neither mechanism can be ruled out, nor need stocks comply to either. Unfortunately, a longer data series for the anchovy population is not possible as prior to 1966 catches were sporadic or reflected the partial introduction of the 12,7 mm net. Similarly for the pilchard population mesh size changes made comparisons before 1966 less precise, however South African pilchard data over the period 1950/1974 fitted a Beverton and Holt curve with a correlation coefficient = 0,54 ($P < 0,01$ with 23 degrees of freedom). Neither data set can include more recent years due to uncertainties in the V.P.A. technique. A longer test series must, therefore, be left to the future.

MIGRATIONS

Introduction.

There is some evidence that both the anchovy and pilchard populations take part in annual migrations. Data on anchovy migrations have not been published, but some of the evidence for these movements will be given here. The annual sardine run has been documented by Baird (1971) and more recently discussed by Crawford and Shelton (1976). The drop in pilchard catch after 1962 (Table I) has been associated with definite distributional changes. (Centurier-Harris and Crawford 1974) These changes amount to a shift in the bulk of the adult pilchard catches from the west coast to a more southerly and warmer region east of the Cape of Good Hope.

The change in distribution of adult pilchard stock parallels one that occurred in the Californian system during the 1950's. Before the collapse of the pacific sardine, the fishery extended from Baja California into the Pacific North west, this was followed by a progressive shift southward with the northern fishery disappearing completely after

1948. By 1966 most landings were from the southern half of Baja California.

Method of Study.

The catch per unit effort (c.p.u.e.) was calculated for each species in each area in each week of the year. The effort was stated in standard boat days for that area-week, where the relative fishing power of vessels was obtained from Newman et al (in press).

The effort was the total effort expended in that area-week, and not the effort directed toward a particular species as no rationale for splitting the effort could be decided upon.

Both anchovy and pilchard populations form mixed species shoals, but larger fish of both species were more often caught in pure shoals east of Cape Point to which area spawning has largely been confined since 1967 (Anders, Sea Fisheries Branch, pers. comm.) Juveniles, often in mixed shoals were more common on the west coast. For this reason c.p.u.e. was calculated for different shoaling types.

Results.

The catch per unit effort figures show that catches of young anchovy and pilchard are made in the north during late summer and progressively southward as the season continues. This suggests that juveniles find their way northwards after being spawned in the south, returning to complete the cycle.

By analogy, a northward movement in juvenile pacific sardine has been noted. "These northward movements occur during the summer months, and a return southward takes place in late fall and winter" Clarke (1952).

The distributional change in shoal type of anchovy and pilchard during the period 1965/1976 is illustrated by the proportion of the catch made west of Cape Point. This is reflected in Figs. 3 and 4 respectively.

The proportion of adult anchovy and pilchard catches made on the west coast decreased markedly over the period 1965/1976. Conversely, juveniles of both species occurring in mixed shoals on the west coast did not show a similar decline.

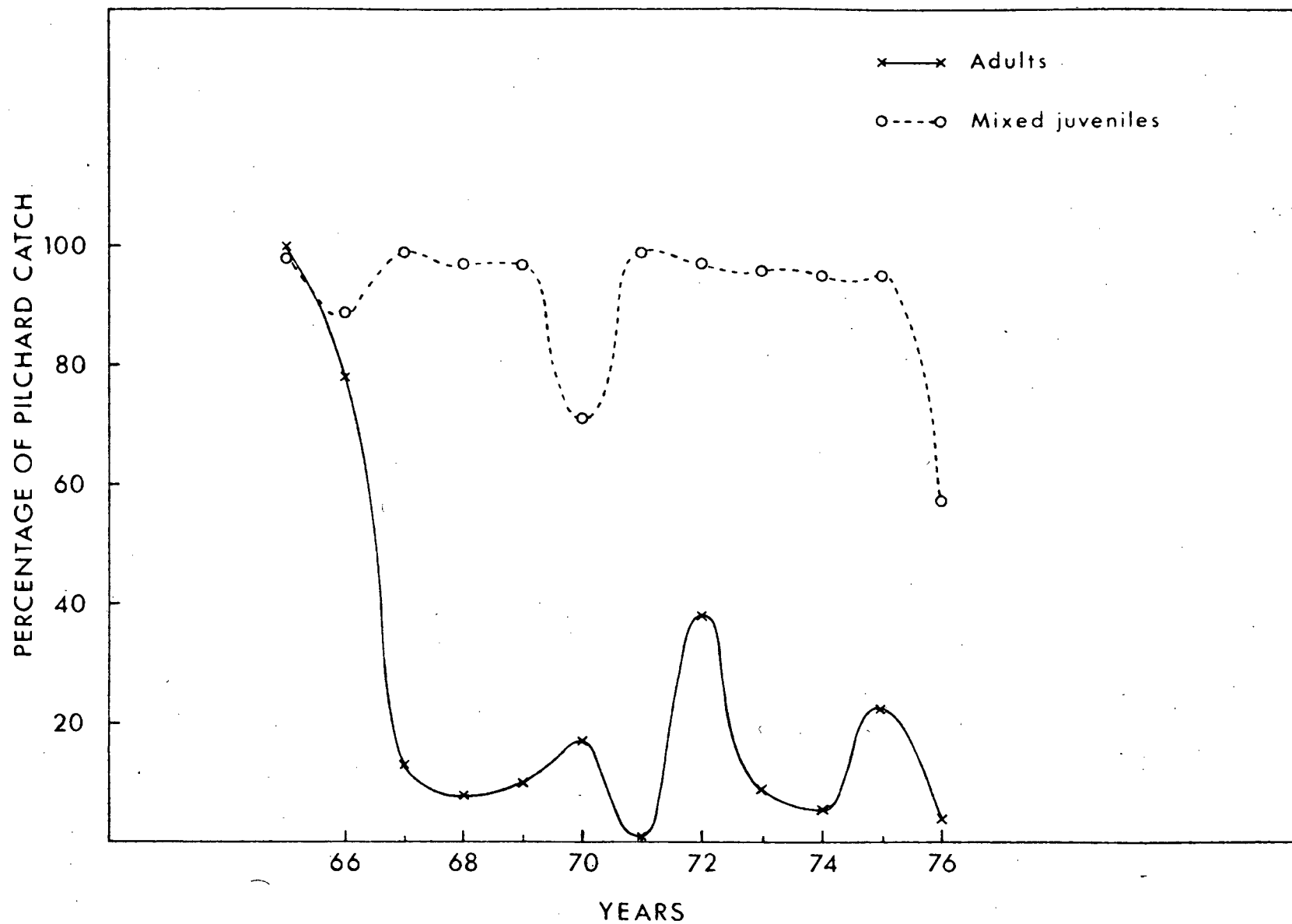


FIG. 3. PERCENTAGE OF PILCHARD CATCH MADE ON THE WEST COAST.

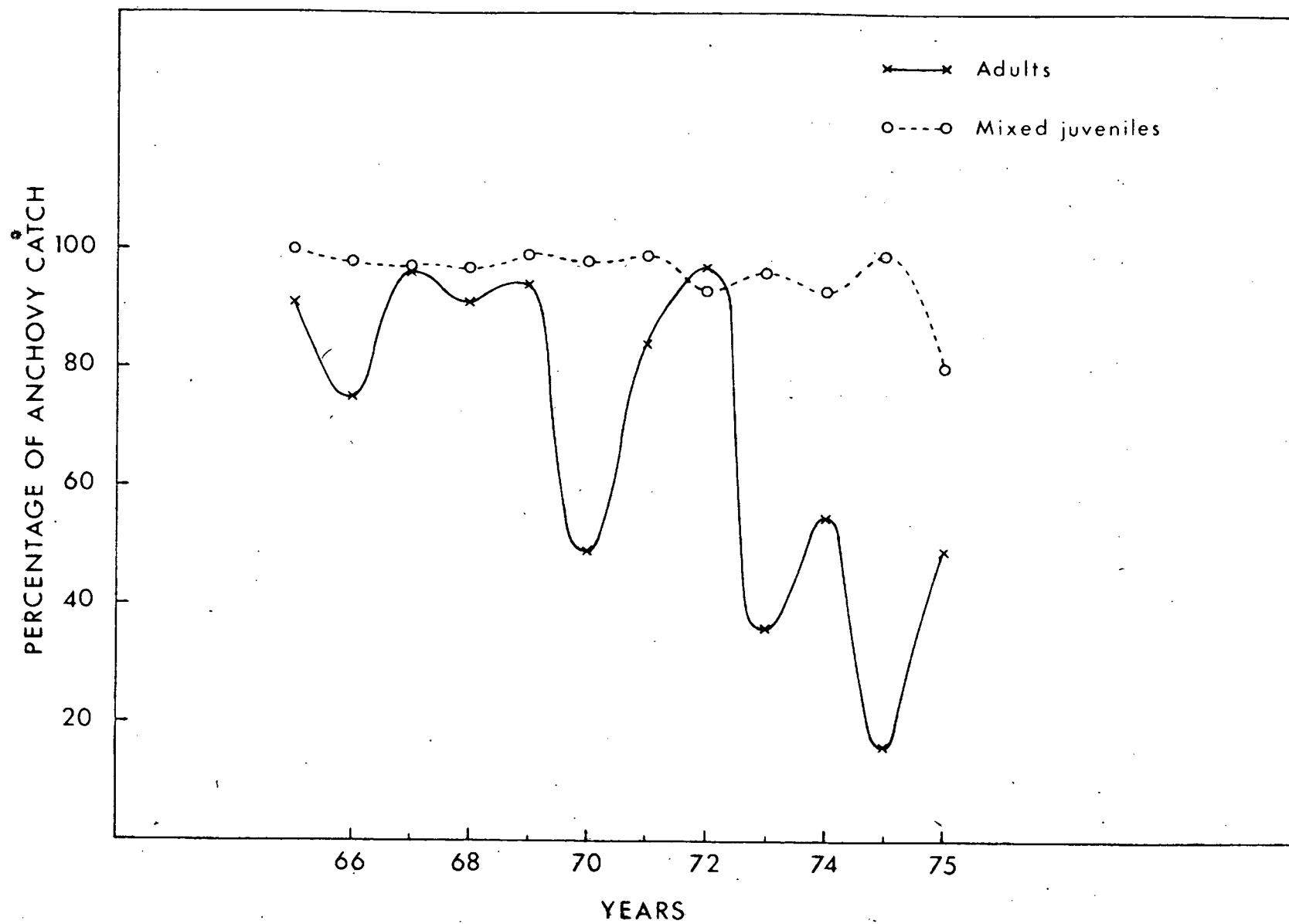


FIG. 4. PERCENTAGE OF ANCHOVY CATCH MADE ON THE WEST COAST.

Indications are therefore that anchovy and pilchard recruitment occurs on the west coast independently of the location of the adult stock. This confirms the c.p.u.e. result and may indicate a migration of larval or juvenile fish to the west coast.

The extent to which these movements are passive drifts is not clear. The June/July sardine run on the Natal coast coincides with a strong counter-current flowing northward. On the west coast juvenile fish probably move passively northward in the Benguela current soon after spawning (L. Hutchings, Sea Fisheries Branch, pers. comm.)

INTERACTION BETWEEN ANCHOVY AND PILCHARD POPULATIONS

Method of Study.

According to the V.P.A. results of a previous section, the pilchard biomass was greatest in 1959, when it exceeded 2 million metric tons.

The size of the anchovy population prior to the introduction of the 12,7 mm mesh net (in 1964/1965) cannot be quantitatively deduced as anchovy did not appear regularly in the catches. Blanket net samples, however, showed that anchovy larvae appeared to be more abundant than pilchard larvae in the years 1961/1965 (Stander and Le Roux 1968).

It is unfortunate that the abundance of both species cannot be compared through the period of greatest change, however, after the full scale introduction of the smaller 12,7 mm net the pilchard population continued to fall whereas anchovy recruitment remained steady or showed a slight tendency to increase after 1965 (Fig. 5).

Environmental data series comparable with historical anchovy and pilchard biomass data have not yet been prepared. Quantitative interaction studies have

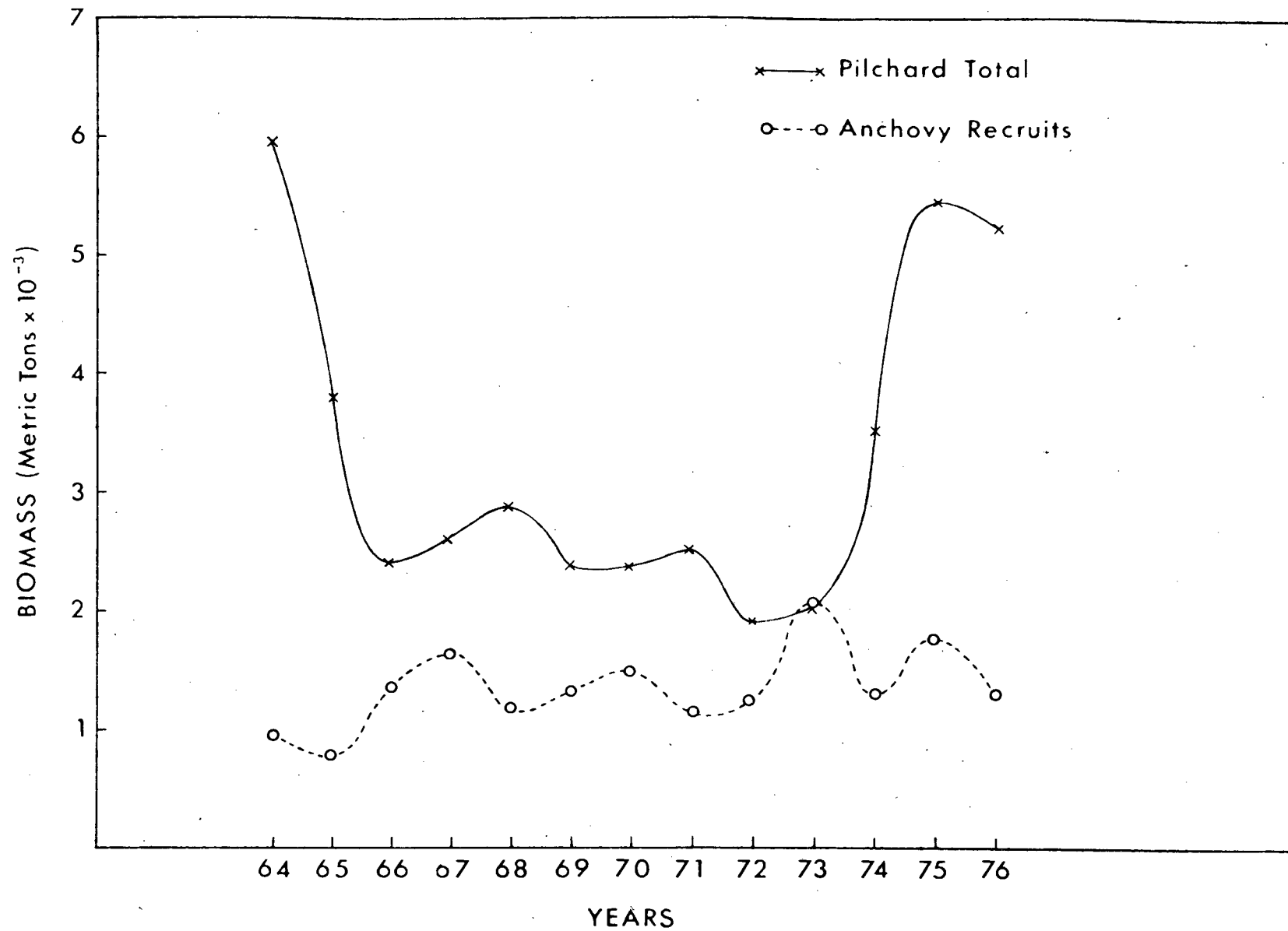


FIG. 5. ANCHOVY RECRUITS AND PILCHARD TOTAL BIOMASS

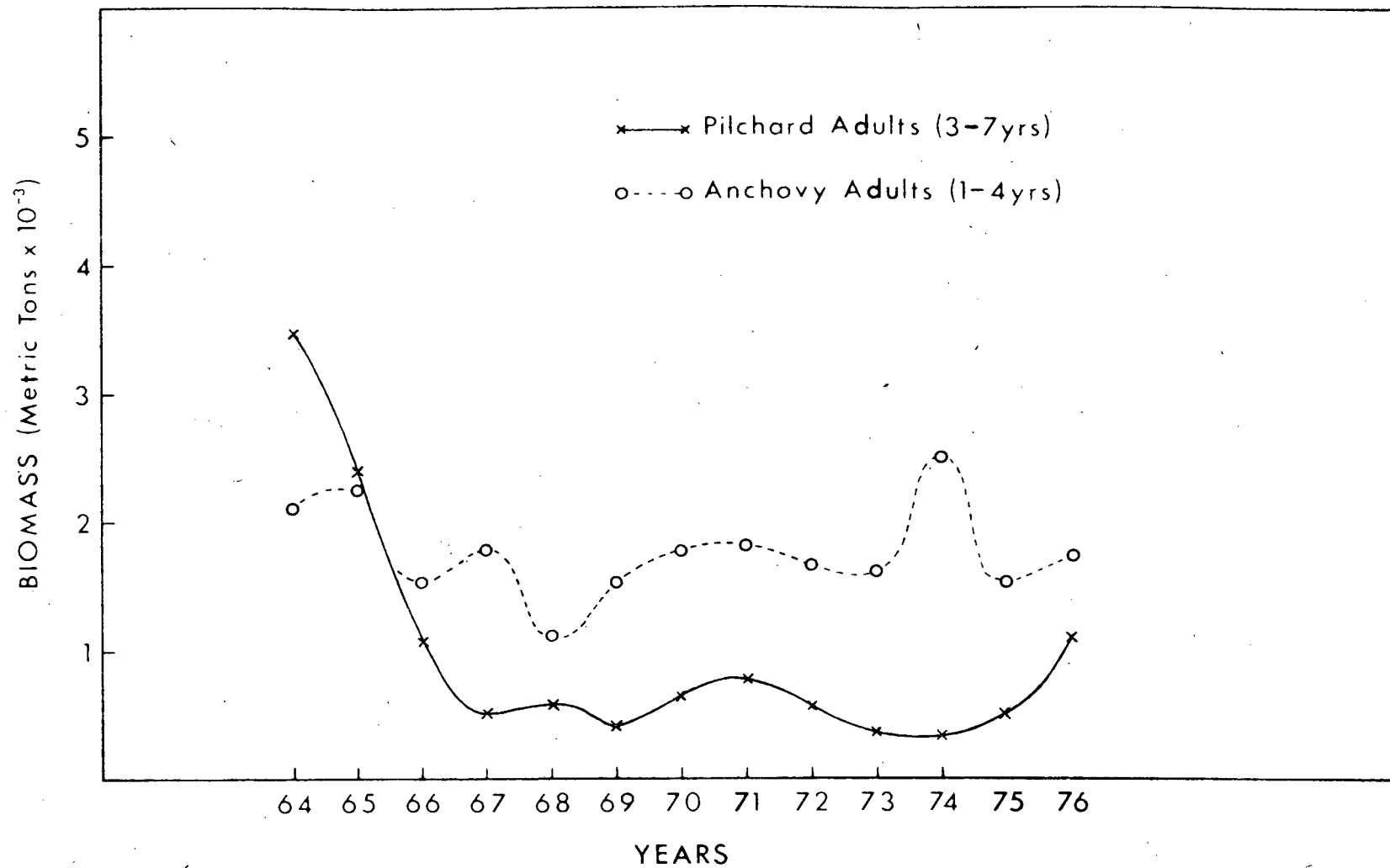


FIG. 6. ANCHOVY AND PILCHARD ADULT STOCK BIOMASS

thus been confined to various age groups of the two stocks which for the purposes of discussion are postulated as competitors.

Three mechanisms might account for the trends in anchovy and pilchard population size:

- (1) The abundance of anchovy and pilchard might be determined by the effect of fishing effort on the density dependent processes of reproduction
 - (2) The anchovy population might be a more efficient competitor or have greater resilience to fishing pressure and environmental factors than the pilchard population
 - (3) The abundance of both species might vary due to different responses to the same environmental conditions
-
- (1) According to Murphy (1966) "In all sardine populations that have been studied, there is clear evidence of large fluctuations in year-class size. These seem unrelated to spawning stock size, and, therefore, are almost certainly a function of the environment."

The environmental factors responsible for the variations in reproductive success are not known. However, a species whose reproductive processes are greatly affected by hydrological conditions can be more easily over-fished than one whose reproductive success is more related to density dependent processes, such a species can also increase rapidly in abundance.

Landings of pilchards in South Africa which dropped 10-fold from 400 000 metric tons in 1961 and 1962 to 41 000 metric tons in 1973 and 16 000 metric tons in 1974, increased to over 160 000 metric tons during 1976, the highest level in 11 years.

V.P.A. indicates that a good year-class of pilchards was entering the fishery in 1974 when no 0 year old fish were recorded in the catches and effort had not been reduced (Tables III and IX). In addition the abundance of anchovy has remained steady and apparently independent of fishing effort since 1964 (Table X). These results indicate fishing effort has not been dominant in determining the abundance of these two populations.

- (2) Stander and Le Roux (1968) suggest that the South African pilchard and anchovy have a common ecological niche and state that "As the two species compete among others, for a common food supply, there is presumably an equilibrium between the respective populations, which is liable to be disturbed by external factors such as the continued high rate of exploitation and reduction in numbers of one of them."

If the anchovy population had shown a stronger response to environmental conditions such as food quality or patchiness, as well as to fishing effort, an increase in abundance concomitant with a decline of the pilchard population might have been expected.

Murphy showed that the reduction of the sardine population off California to one tenth of its former size was an important event in the food chain. This conclusion was reached after the total calorific need of the pilchard for growth and respiration had been estimated from the standing crop of fish and the mean energy consumption. The total calorific requirement per annum was found to be equivalent to about 3,5 times the standing crop of

zooplankton, which even allowing for a reasonable import of additional food through advection represented a considerable proportion of the possible turnover rate of zooplankton in the California current area, thought to be no greater than 5 times per year.

The reduction of the pilchard population in Cape waters was of the same order, and was probably of similar importance in the economy of the Cape trophic system.

There is, however, little evidence to suggest that the anchovy population was responsible for or responded to the decline in pilchard abundance (Fig. 6).

In particular there is no evidence of unusually strong anchovy recruitment during the years 1964/1972 when it might have been expected (Fig. 5).

- (3) Environmental changes have been shown to have a direct bearing on a Southern African pelagic ecosystem :

Stander and De Decker (1969) observed an anomalous physical condition in South West Africa during 1963, which resulted in marked faunistic changes. The changes were characterized by a disruption of the annual

temperature pattern which had an impact on plankton, oil yield and survival of fish larvae.

Southward et al (1975) reasoning that a large part of the solar energy budget is mediated through the surface of the oceans have analysed sea temperatures in the English Channel and various biological measurements in the vicinity. Major cycles in mean surface temperatures of the order of 10-11 years were found using a 5-year running average. These show close agreement with curves depicting sunspot number. Biological data indicated the presence of similar 11 year cycles in such features as the number of pilchard eggs, the catch of demersal fish, and the proportions of barnacle species in the intertidal zone.

Fluctuations and large scale changes in marine organisms have been shown by several authors. Reid (1975) has investigated phytoplankton changes in the North Sea, and Coomb (1975) has worked with larval fish abundance in the same area; both authors found a change in the waters of the North Western Atlantic during 1965/1967 which it is believed might have affected most pelagic organisms. The widespread pattern of

change probably had its origin in climatic events but these were not established.

Long term trends in South African pelagic fish population biomass are not available. However, guano production records have been made since the beginning of the century. Guano production after 1950 showed good correlations with pilchard biomass suggesting that guano production may be an index of the abundance of fish available to the birds (Crawford and Shelton in prep.)

Although not definitive some indication of long term cycles in guano production is evident.

Anchovy and pilchard probably have very similar food requirements (Davies 1957; King 1976).

Anchovy were found to change from zooplanktophagous to phytoplanktophagous feeding at a standard length of 80 mm whereas pilchard made the same change at 100 mm standard length. This suggests that if the anchovy is a more efficient competitor for food changes in abundance are a subtle response to the quality or patchiness of the food. Reproductive efficiency may also be influenced by changes in hydrological conditions.

Of the three hypotheses discussed above, the first seems to be the least applicable. The anchovy population has proved to be remarkably unaffected by the effort directed towards it. Annual landings of anchovy have remained over 200 000 metric tons since 1971, while the population size over the same period is estimated by V.P.A. to be approximately 300 000 metric tons. Pilchard landings have fluctuated sharply in the face of continually increasing fishing effort as noted above. In order to establish which of the three hypotheses is the most likely, factors affecting the biomass need to be compared in a quantitative way.

Regression Analysis.

A multiple linear regression analysis was used to determine whether the variation in abundance of the anchovy and pilchard populations can be understood in terms of the stock sizes and total fishing effort.

V.P.A. estimates the abundance of a stock at each age group, and the abundance of age groups of each species may be compared in the same year or between

successive years.

The more factors that are contained within a test, the greater the chance of including effective ones, but the longer the series necessary to establish the correlation between them. To overcome this difficulty a step wise multiple linear regression was used. Using this method only those variables which explain the variance of the dependent variable to a specified extent are retained in the analysis.

Factors can be separated in a step wise multiple regression showing the order in which they contribute to the variance of the dependent variable. This is valid even if the factors are not independent of each other. (Snedecor and Cochran 1972)

Care is necessary when deducing casual relationships from correlations. In these cases a third undetected factor may be responsible for the apparent association. On the other hand when there is a large variability of unknown origin multiple regression separates the components quantitatively so that residual error is reduced.

Three step wise multiple linear regressions were carried out :

- (1) In a preliminary investigation the total biomass

of pelagic species were compared during the period 1964/1975; the pilchard biomass was regressed against that of anchovy, red-eye, mackerel and the total biomass of these species including maasbanker which occurred irregularly. Total fishing effort was included in the regression.

- (2) The hypothesis that the biomass of anchovy and pilchard populations are independent was tested. Anchovy biomass was regressed against the biomass of various age groups of the pilchard population, as well as total fishing effort.
- (3) The anchovy biomass is largely comprised of fish less than 1 year old. The effect of a previous years pilchard stock on anchovy recruitment was therefore tested in a multiple regression of the same form as (2).

The calculations were carried out on a UNIVAC model 1100 computer using STEPREGI, a program developed by Madison Computing Centre.

Results.

(1) The first regression had the form :

$$PB = mAB + nRB + rMB + sTB + pEFF + qY + c \quad (18)$$

where PB = biomass of pilchard

AB = biomass of anchovy

RB = biomass of red-eye

MB = the biomass of mackerel

TB = the total biomass including maasbanker

EFF = the total fishing effort

Y = the year of the estimate and

m,n,r,s,p,q, and c = constants

The data used for analysis and the results are presented in tables XVI and XVII.

TABLE XVI

DATA FOR REGRESSION OF PILCHARD BIOMASS ON ANCHOVY,
RED-EYE, MACKEREL AND TOTAL BIOMASS ESTIMATED USING
V.P.A. (metric tons x 10^3) AND TOTAL FISHING EFFORT
(Standard boat days x 10^2)

	PILCHARD PB	ANCHOVY AB	RED-EYE RB	MACKEREL MB	TOTAL TB	EFFORT EFF	YEAR Y
	598	314	22	83	419	55	1964
	382	306	35	60	403	96	1965
	243	289	48	144	489	81	1966
	259	343	58	251	666	121	1967
	286	246	52	201	500	111	1968
	241	287	47	160	496	103	1969
	235	326	62	108	500	111	1970
	254	295	57	89	473	101	1971
	189	290	50	103	446	131	1972
	203	370	43	101	518	122	1973
	350	384	25	84	507	87	1974
	550	332	35	92	459	103	1975
Mean	316	315	45	123	490	102	1970
Variance	17 654	1 483	165	3 145	4 371	425	13

TABLE XVII

DETAILS OF MULTIPLE LINEAR REGRESSION OF TOTAL BIOMASS

	SOURCE OF VARIANCE						
	AB	RB	MB	TB	EFF	Y	c
Regression Coefficient	2,15	-2,17	2,50	-2,35	-3,06	5,40	-9 741
Std. error of Regression Coefficient	5,31	9,27	4,84	4,83	3,36	15,03	29 386
Partial Correlation Coefficient	0,18	-0,10	0,23	-0,21	-0,38	0,16	-0,15
T-value with 5 degrees of freedom	0,41	-0,23	0,52	-0,49	-0,91	0,36	-0,33
Significance Level	0,70	0,82	0,63	0,65	0,40	0,73	0,75

	REGRESSION		RESIDUALS	
	All Variables	Significant Variables	All Variables	Significant Variables
Mean square	20 868,9	89 240,9	13 796,9	10 495,7
F ratio	1,51	8,50		
Degrees of Freedom	6	1	5	10
Significance	0,33	0,02		
Coefficient of determination	0,64	0,46		

With all variables included in the regression the null hypothesis that pilchard biomass is not accounted for in terms of the independent variables was therefore accepted for the period concerned.

When variables which did not contribute to the variance of the equation to a significant extent were excluded, only total effort was retained. However the coefficient of determination (the square of the multiple correlation coefficient) indicated that only 46 per cent of the total variation in pilchard biomass was explained by the total effort during the 12 year period considered. The biological implications of these results are discussed in the next section.

- (2) The second regression attempted had the form :

$$AB = aPRB + bPMB + cPAB + dPTB + eEFF + gY + h \quad (19)$$

where AB = anchovy biomass

PRB = pilchard recruit biomass (0 years old)

PMB = pilchard biomass of 1 and 2 year old fish

PAB = pilchard adult biomass (3 years and older)

PTB = pilchard total biomass

EFF = total fishing effort

Y = year of estimate

a,b,c,d,e,g,h, = constants

The data used for analysis and the results are presented in Tables XVIII and XIX.

TABLE XVIII

DATA FOR THE REGRESSION OF ANCHOVY BIOMASS ON PILCHARD BIOMASS ESTIMATED USING V.P.A. (m.tons $\times 10^3$) AND TOTAL FISHING EFFORT (standard boat days $\times 10^2$)

	ANCHOVY		PILCHARD			EFFORT	YEAR
	AB	PRB	PMB	PAB	PTB	EFF	Y
	289	49	87	108	243	81	1966
	343	97	111	52	259	121	1967
	246	97	130	60	286	111	1968
	287	59	141	42	241	103	1969
	326	58	111	65	235	111	1970
	295	84	94	76	254	101	1971
	290	40	92	57	189	131	1972
	370	97	70	37	203	122	1973
	384	167	148	35	350	87	1974
	332	128	369	53	550	103	1975
Mean	316	88	135	59	281	107	1971
Variancel	801	1 518	7 355	463	10 896	241	9

TABLE XIX

DETAILS OF MULTIPLE LINEAR REGRESSION OF ANCHOVY
BIOMASS ON PILCHARD BIOMASS

	SOURCE OF VARIANCE							h
	AB	PRB	PMB	PAB	PTB	EFF	Y	
Regression								
Coefficient	-7,07	-7,76	-7,97	7,59	-0,16	4,05	-7	644,5
Std. error of								
Regression	29,65	29,74	30,12	29,75	1,56	9,51	18	734,3
Coefficient								
Partial								
Correlation	-0,14	-0,15	-0,15	0,15	-0,06	0,24	-0,23	
Coefficient								
T-value with								
3 degrees of	-0,24	-0,26	-0,26	0,26	-0,10	0,43	-0,41	
freedom								
Significance								
Level	0,83	0,81	0,81	0,82	0,92	0,70	0,71	

	REGRESSION		RESIDUALS	
	All Variables	Significant Variables	All Variables	Significant Variables
Mean square	1 462,4	-	2 479,0	-
F ratio	0,59			
Degrees of				
Freedom	6	-	3	-
Significance	0,73	-	-	-
Coefficient of	0,54	-	-	-
determination				

With all the variables of equation (19) included in the regression, the null hypothesis that anchovy biomass is not accounted for in terms of pilchard stock abundance is therefore accepted for the 10 year period concerned. With the exclusion of statistically insignificant variables (at the 5 per cent level) all independent variables were eliminated. No step wise comparison was therefore possible. A biological interpretation of the results of the regression equation (19) is given in the next section.

- (3) Results showed that the contribution of the variables of the third regression in explaining the overall variability of the equation was not significant according to the F test. Similarly using Students t test the coefficients were not statistically significant.

When variables which did not explain the variance in anchovy biomass to a significant extent were excluded from the equation, all independent variables were again eliminated. No step wise comparison was therefore possible.

DISCUSSION AND CONCLUSION

Sustainable Yield.

The concept of a sustainable yield for pilchard has been questioned by Murphy (1966) who expressed the view that the population required to produce a certain yield would release resources to the anchovy which, increasing, would change the environment of the pilchard population and hence its sustainable yield. Larkin (1977) has highlighted the fact that population interactions would seriously undermine the concept of a sustainable yield. This author pointed out that the complex interrelationship between mackerel and herring shown by Lett and Kohler (1976) might be typical of other fish communities. Environmental causes of year-class strength are not well enough understood to allow predictive and remedial measures to be enforced to conserve the stock. There appears to be a considerable amount of mortality occurring within a year-class independently of fishing effort, rendering a maximum sustainable yield unreliable. This is shown by the low coefficient of determination (Table XVII) and trends in effort and abundance (Fig. 7).

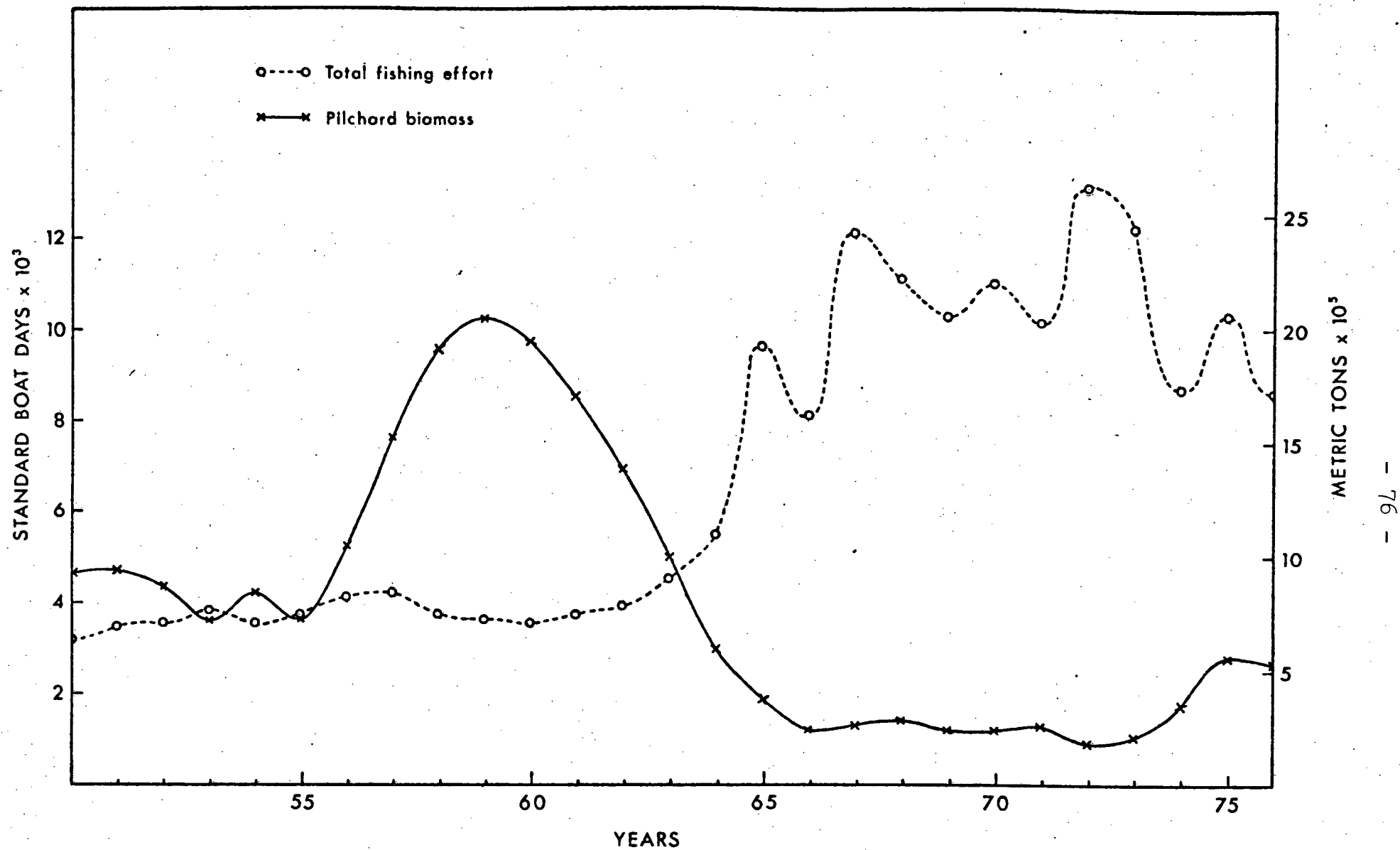


FIG. 7. PILCHARD BIOMASS (METRIC TONS) AND TOTAL FISHING EFFORT (STANDARD BOAT DAYS)

Fishing pressure on the pilchards has not been deliberately reduced, however it is probable that as the population decreased it became less available and therefore subject to less fishing mortality, forming a negative feed-back system. The more available species, especially the anchovy, probably absorbed the effort previously directed to the pilchard. This would allow the pilchard population to endure several years of poor environmental conditions to produce strong year-classes once again.

Abundance Estimates.

Trends in population abundance obtained by V.P.A. have been compared to catch per unit effort analysis (Newman et al in press and Stander and Le Roux 1968). From Table XI it can be seen that the biomass of the pilchard population reached a peak in 1959, whereas abundance according to catch per unit effort peaked in 1961 when the strong cohorts which comprised mainly young fish in 1959 had become more available to the fishery as older age groups. Pilchard biomass declined from approximately 2 million metric tons in 1959 to about 200 000 metric tons in the mid 1970's. This trend was confirmed by the c.p.u.e. results. Subsequently 1974/1975 pilchard biomass rose to over

500 000 metric tons (Table XI). On the other hand, the anchovy population remained relatively constant at a level of about 300 000 metric tons (Table X). Trends in the anchovy and pilchard biomass are not affected by the assumptions about exploitation rate and natural mortality as shown in Tables VI, VII, X and XI.

Trends in abundance of fish populations should be seen against the background of a possible cycle in hydrological conditions. This would help explain the appearance of large and small year-classes, especially where they appear independently of fishing effort. In order to demonstrate that there are long term cycles in hydrological conditions long sequences of information are required. Hydrological data has not yet been accumulated for long enough in South African waters to show whether or not there are long term cycles.

Factors influencing fish populations.

- (a) Stock-recruit relationships. South African data on the anchovy and pilchard populations were fitted to the Ricker (1975) and Beverton and Holt (1957) stock-recruit curves. The two models have a common basis at low rates of

population growth (Eberhardt 1977) but the form of the curves generated by a least squares fit of anchovy population data was very different (Fig. 1) indicating that the anchovy may have a high rate of growth at low stock levels. However, stock levels of the anchovy population low enough to test this hypothesis have not been recorded. The curves generated by a least squares fit of pilchard population data are shown on Fig. 2. According to Ricker (1975) a fit to the Beverton and Holt curve suggests the environment is more important controlling influence than stock density.

(b) Interaction.

The question of which stage of the life history of fish is most liable to cause mortality and hence changes in abundance, has occupied biologists for many years. Ricker (1954) was the first to suggest that recruitment was a continuum starting with the fecundity of the adult stocks and followed by interspecific competition and cannibalism by the parent stock. Most marine fishes are very fecund, producing between 10^4 and 10^7 eggs per female, and it is generally recognised that control of numbers in fish populations is achieved by processes dependent on density in juvenile life rather

than by variations in fecundity in adult life (Harris 1975; Cushing 1975).

(c) Mechanisms

In this thesis three possible mechanisms controlling anchovy and pilchard abundance are discussed in the light of the results of a regression analysis. Mechanism (1) in which abundance is considered as dependent on effort is tested for the anchovy population in equation (19) and the pilchard population in equation (18).

Fig. 7 shows that total fishing effort was considerably lower before 1966, and it is unfortunate that the anchovy abundance cannot be compared with effort during that period. However for the period 1966/1975 total fishing effort is not significant in explaining the variance in anchovy biomass (Table XIX). This suggests that the first mechanism is not dominant.

The coefficient of determination indicated that only 46 per cent of the variation in pilchard biomass is explained by the total fishing effort during the twelve year period considered.

Similarly a longer series (Fig. 7) shows that pilchard abundance is negatively correlated with total fishing effort of the same year.

$$r = -0,75 \text{ (} P < 0,01 \text{ with 25 degrees of freedom)}$$

Mechanism (2) which implies that there is some competition for food between the anchovy and pilchard is not substantiated by equations (18) or (19). The variation in pilchard abundance was not significantly correlated with the abundance of other pelagic species in equation (18), it is therefore concluded that anchovy abundance is not likely to influence the parameters of the pilchard population that describe its abundance, contrary to the view of Murphy (1966). This is substantiated by Figs. 5 and 6 which show that although the pilchard biomass dropped considerably in 1965 no increase in anchovy recruit biomass took place. After 1965 the anchovy recruit biomass increased marginally while pilchard biomass continued to fall. Any increase in the anchovy population is thus a secondary event. A similar observation was made for the Californian sardine population where the anchovy succeeded the pilchard with a definite time lag (Murphy 1966).

Variation in anchovy abundance was also not significantly accounted for by pilchard stock size (equation 19) indicating that the two stocks are independent.

Cushing (1975) considered density dependent mortality to be a continuous and fine control of recruitment being modulated by the availability of food which could include quality or patchiness of the food. In this way density dependent processes are exploratory, and the carrying capacity of the environment is exploited continuously. This seems possible for the anchovy and pilchard populations in South African waters, and in this sense mechanism 3 is the most likely.

The results of this thesis show that the size of the pilchard population has been influenced by fishing effort during the period 1950/1974. This is not of academic interest only, as financial benefit would accrue from equilibria favouring the dominance of large cannable pilchards. However, the mechanisms controlling species abundance are not fully understood, and indications are that understanding of abundance

rests on more adequate understanding of the environment. Rational management of the stocks should therefore include indicators of environmental suitability and stock recruit relationships. Research should be directed toward understanding parts of the life cycle most susceptible to both biotic and abiotic conditions, including the pre-recruit phase. However predictive theory will only progress with synthesis of population dynamics and ecology (Russell-Hunter 1970).

The simple exploitation of all pelagic species, with emphasis on the dominant one seems to provide the logical means of maintaining an equilibrium as well as taking advantage of good year-classes. The correct emphasis could be applied through the allocation of an annual quota for each species. A separate quota system for anchovy and pilchard catch would give a more flexible control of fishing effort, allowing effort to be directed when advantageous to species such as the anchovy which appear to be less sensitive to it.

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STOCK ASSESSMENT OF THE HAKE (Merluccius capensis and Merluccius paradoxus)
ON THE CAPE OF GOOD HOPE FISHING GROUNDS (ICSEAF DIVISION 1.6)

EVALUATION DU STOCK DE MERLUS (Merluccius capensis et Merluccius paradoxus)
DES LIEUX DE PECHE DU CAP DE BONNE ESPERANCE (DIVISION 1.6 DE LA CIPASE)

EVALUACION DE LA POBLACION DE MERLUZA (Merluccius capensis y Merluccius paradoxus) DE LOS CALADEROS DEL CABO DE BUENA ESPERANZA
(DIVISION 1.6 DE CIPASO)

by/par/por

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A. INTRODUCTION

Catch and effort statistics for bottom trawlers on the Cape of Good Hope fishing grounds (ICSEAF Division 1.6) are available for hake since 1955 (Table 1) and show that the catch has risen steadily during this period. Previous attempts to assess the stock (Anon. 1973) have indicated that the hake population on these grounds could at present be fully exploited.

Two species of hake are caught, Merluccius capensis and Merluccius paradoxus, but they have not always been distinguished in catch-per-unit-effort, size- and age-composition information. For assessment purposes the two species have consequently been considered as one stock. The growth parameters for the two species are similar (Anon. 1973), so that their treatment as a single stock should have some validity.

In view of the recent increase in catches in Division 1.6 it is important that the maximum sustainable yield from the fishing grounds be established, together with the optimal amount of effort required to harvest it. In this report an attempt has been made to ascertain the maximum sustainable yield using various techniques. Initially virtual population analysis was applied to determine stock size, recruitment and fishing mortality. From this information an equilibrium yield per recruit curve was established. Secondly, stock production curves were fitted to catch and effort data and from these curves yield and stock sizes at different levels of effort were calculated. Finally, the results of these two analyses were compared to a relationship obtained from a plot of catch-per-unit-effort on the mean effort of the two previous years.

The techniques used in the above analyses require assumptions about certain parameters, notably natural mortality and catchability coefficients. Sensitivity analysis was therefore conducted to determine how critical these assumptions were to the estimations of yield and stock size by the methods used in this paper.

B. VIRTUAL POPULATION ANALYSIS

1. Method and sensitivity

The weights of hake landings from catches made on the Cape of Good Hope grounds were converted to numbers of fish caught following the method of Draganik (1974). Essentially this consisted of using information on age frequency and weight at age from each contributing country, to determine the numbers of fish caught in each age group, according to the expression:

$$C_n = \frac{S_n \cdot Y}{\sum_n (S_n \cdot w_n)} \quad (1)$$

where C_n = the number (in millions) of fish of age n which are caught in that year,

S_n = the frequency with which fish of age n occur in the samples,

Y = the annual catch (in metric tons)

and w_n = the weight (in grams) of a fish of age n , as given by the country providing the age frequency data.

The catches of nations which did not submit age composition data were allocated to those countries with adequate information, in proportion to the catch weights of these contributing countries. The numbers of fish from each age class that were caught in each year appear in Table 2.

Estimates of the fishing mortality and total numbers of fish in the population for each age class were then obtained by the technique of Gulland (1965). The number of individuals alive is calculated by the expression:

$$x_n^N = \frac{x_n^C \cdot x_n^Z}{x_n^F (1 - e^{-x_n^Z})} \quad (2)$$

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where x_n^N = the number of fish at age n from year class x ,

x_n^C = the number of fish caught at age n from year class x ,

x_n^F = the fishing mortality on fish of age n from year class x ,

and x_n^Z = the total mortality on fish of age n from year class x .

x_n^Z was determined as the sum of $x_n^{F_n}$ and M (the natural mortality coefficient). This latter was assumed to be constant with a value of 0.25 (Draganik 1974). The technique also requires the assumption of a terminal fishing mortality value for each year class, the fishing mortality on the oldest age group in the year class for which information is available. All other fishing mortality values are found by iteration from the following equation:

(3)

$$\frac{x_{n+1}^N}{x_n^C} = \frac{x_n^Z e^{-x_n^Z}}{x_n^F (1 - e^{-x_n^Z})}$$

The selection of suitable terminal fishing mortalities for each age class was complicated, for not only did assumptions have to be made about the mortalities inflicted on those age groups which were fully selected, but a pattern of selection also had to be established in order to calculate the terminal fishing mortalities to which the younger age groups were exposed. Therefore an initial virtual population analysis, using the terminal fishing mortalities and patterns of selection which were adopted by Draganik (1974), was conducted. An examination of the resulting pattern of fishing mortality values in earlier years, when they would not be sensitive to Draganik's assumptions, suggested that the following selection pattern would be more appropriate:

Age	3	4	5	6	7
Per cent selection	15	30	50	70	100

From this it appears that hake in ICSEAF Division 1.6 are only fully selected at an age of 7 years. The actual fishing mortality value considered to be appropriate for the fully selected age classes was 1.7. This is a high value, but it was chosen after repeating the virtual population analysis for a series of terminal fishing mortality values on fully selected age groups, because it produced a change in fishing mortality patterns which was roughly proportional to the change in fishing effort observed in recent years.

Estimates of $x_n^{F_n}$ for the years 1968, 1970, and 1972 are listed in Table 3 for three different choices of terminal fishing mortality. The ratios of the two extreme assumptions, that is $F_n \geq 7 = 1.2$ and $F_n \geq 7 = 1.8$, appear in the last column of the table. It is clear that the estimates of $x_n^{F_n}$ are not sensitive to the initial choice of terminal fishing

mortality at least up until 1970. The low sensitivity of $x_n^{F_n}$ suggests that estimates of stock biomass would be equally robust with regard to initial assumptions of terminal fishing mortality. Table 4 confirms that this is indeed so.

The sensitivity of the model to assumptions concerning the natural mortality coefficient (M) was examined by repeating the virtual population analysis for $M = 0.1$; $M = 0.25$; and $M = 0.3$ (Table 5). These values were chosen as a possible range around the value of 0.25 established by Draganik (1974). The ratio of stock biomass estimates for the extreme values of $M = 0.1$ and $M = 0.3$ are such that these estimates must be regarded as being sensitive to assumptions concerning the natural mortality coefficient.

2. Catchability coefficient

The catchability coefficient (q) can be derived from the equation:

(4)

$$F = qf$$

where F = the fishing mortality coefficient,

and f = the fishing effort.

However, the calculation of q was complicated by the fact that a number of age classes of hake, although exploited, were not fully selected by the fishing gear used, as is shown on Table 6. Values of F , and therefore q , depend on age.

Table 6 confirms, though, that hake of seven years and older, were subject to full selection. The q values for fish aged seven to nine inclusive were consequently calculated for each year by means of equation (4) and have been listed on Table 7. They are reasonably consistent and of the order of 0.00005. The fishing mortalities used were the averages for hake, between the ages of seven and nine. Fish aged ten and older were ignored as there were insufficient numbers in the catch of these age groups to permit a reliable estimate of mortality.

Hake which are younger than seven years, however, contribute large numbers to the catch, so that, in order to obtain a value of q which was applicable to the hake stocks generally, the following procedure was adopted. The average weighted value of fishing mortality (\bar{F}) for all exploited age classes during the period 1965 to 1969 was calculated from the relationship:

(5)

$$\bar{F} = \frac{\sum_{x,n} x_n^F \cdot x_n^C}{\sum_{x,n} x_n^C}$$

The period 1965 to 1969 was selected as in these years the effort expended remained fairly constant (Table 1), averaging 19,824 units. Utilising the information shown on Tables 2 and 6 a value of $\bar{F} = 0.51$ was obtained by this method.

This, when associated with the average fishing effort of 19,824 units, gives $q = 0.00003$ using equation (4). This q value was considered as that most likely to apply to the total exploited hake population and was consequently adopted for the stock production model which is considered in a later section.

3. Fluctuations in recruitment

The numbers of fish in each age group on the Cape of Good Hope fishing grounds are shown, for each year, on Table 8. To illustrate recruitment patterns the numbers of three-year-old fish have been plotted on Figure 1. It may be noticed that from 1964 to 1970 recruitment was very consistent but that thereafter it apparently increased substantially. There is some uncertainty about the validity of the increase because the analysis is less vigorous in later years where the year classes are short. In these cases equation (3) becomes less precise for recruits as x_{N+1} is more closely tied to mortality assumptions. In addition the practice of discarding young fish has decreased, and this may account for some of the observed increase in abundance of recruits.

C. GENERALISED STOCK PRODUCTION MODEL

A generalized stock production model was fitted to the catch and effort information listed on Table 1. This model, which has been fully described by Pella and Tomlinson (1969), is based upon the relationship:

(6)

$$\frac{dP(x)}{dx} = HP'(x) - KP(x) - qf(x)P(x)$$

where $P(x)$ = the biomass of fishable stock at time x ,

H , K and L are coefficients defining the inherent potential for population growth,

q = the catchability coefficient,

and $f(x)$ = the number of units of fishing effort operating on the the population at time x .

The model enables H , K and q to be calculated for a series of values of L , by adopting an iterative procedure to minimise the difference between the observed and predicted catches in each year.

The analysis requires the user to provide initial guesses of the following parameters:

f opt, the optimal fishing effort;

r , the ratio of the stock size at the time when the fishery first comes under observation to the maximum stock size;

U max, the catch per unit of effort when the stock is at its maximum size, and

q , the catchability coefficient.

Likely limits for the above parameters are also required and these, together with the initial guesses, are listed on Table 9.

The model is sensitive to q and may not always be a good estimator of this coefficient. Pella and Tomlinson (1969) suggest, therefore, that if a good estimate of q is available, this should be fixed in the iteration. Accordingly a value of 0.00003 was adopted for q . The derivation of this value has been described in an earlier section.

The coefficients calculated by the model for some selected values of L are listed on Table 10, together with a measure of the goodness of fit (R), which is obtained from the equation:

(7)

$$R = \frac{\sum_{x=1}^a (Y_x - \bar{Y})^2 - \sum_{x=1}^a (Y_x - \hat{Y}_x)^2}{\sum_{x=1}^a (Y_x - \bar{Y})^2}$$

(Pella and Tomlinson 1969)

where a = the number of years for which catch and effort data are supplied,

Y_x = the observed catch for year x ,

\bar{Y} = the mean catch, and

\hat{Y}_x = the predicted catch for year x .

The value of R reflects that proportion of the total variation in the catches which is accounted for by the model.

Once the parameters of the model are known, equilibrium yields and the population sizes which provide these equilibrium yields may be calculated for different levels of effort. The equilibrium yields may be derived from the equation:

(8)

$$Y' = \frac{q \cdot f \cdot (q \cdot f + K)}{H} \left(\frac{1}{L - 1} \right)$$

(Pella and Tomlinson 1969)

where Y' = the equilibrium catch.

For selected values of L , the equilibrium yields at different levels of effort were calculated from this relationship. These have been plotted on Figure 2. The curves suggest that, irrespective of the value of L , the maximum sustainable yield is in the region of 150,000 metric tons per annum. It is also apparent that approximately 25,000 standard South African sidetrawl days are required to capture this amount of fish.

Under equilibrium conditions the catch is related to the population size by means of the equation:

(9)

$$Y' = qfP'$$

where P' = the equilibrium population size.

This relationship enables the population size at a given level of effort to be calculated. At 25,000 units of effort the equilibrium yield is of the order of 150,000 metric tons (Figure 2). Assuming a q value of 0.00003, the size of the exploitable stock providing this yield would then be 193,000 metric tons. At 20,000 units of effort the equilibrium yield would be 135,000 metric tons and the size of the exploitable stock 225,000 metric tons.

Fishing mortality of hake 3 years and younger is low (Table 6) and a small proportion of them is landed. Estimates from the stock production model should therefore be compared to the virtual population estimates of fish 4-years and older. The latter appear on Table 5 for different values of natural mortality. In recent years these estimates have been of the same order, though higher, than those provided by the generalized stock production model.

D. YIELD PER RECRUIT ANALYSIS

As information on fishing mortalities and recruitment was available from virtual population analysis a yield curve was generated by means of the function:

$$(10) \quad Y' = \sum_{n=3}^{10} \frac{F_n}{Z_n} (1 - e^{-Z_n}) \cdot N_r \cdot (e^{-\sum_{x=3}^{n-1} Z_x}) \cdot w_n$$

where N_r = the number of recruits, that is the number of three-year-old hake.

The average fishing mortalities at age for the period 1965 to 1969 (Table 6) were calculated and associated with the average level of effort during the same period, that is 19,824 units (Table 1). The period 1965 - 1969 was selected as during these years the effort remained fairly constant. Fishing mortality values at other levels of effort were estimated by adjustment of these mean values by direct proportion.

A natural mortality value of 0.25 was adopted to calculate the total mortality coefficients and the number of recruits was assumed to be 232 million individuals, the mean value of three-year-olds for the period 1965 to 1969 (Table 8). The weights at age were taken as the mean of those listed for Japan, South Africa and the U.S.S.R. on Table 14 of Draganik (1974).

The resultant curve, which appears on Figure 3, applies to a period in which a stable recruitment pattern prevailed. It suggests that a yield of 144,000 metric tons per annum is available from the stock and that this could be harvested with about 10,000 units of effort. The equilibrium catches decrease only slowly with increasing effort, however, suggesting that the yield is not too sensitive to overfishing.

E. CATCH PER UNIT EFFORT AND EFFORT RELATIONSHIP

The catch and effort data on Table 1 were used to derive the equation:

(11)

$$L_n \left(\frac{Y}{F} \right) = -0.000038 \bar{F}_{x-1, x-2} + 2.67$$

where $\bar{F}_{x-1, x-2}$ = the average fishing effort for the years $x-1$ and $x-2$.

The correlation coefficient was -0.93 which with 17 degrees of freedom is significant at the 1 per cent level. Equation (11) was then used to calculate equilibrium catches at different levels of effort and these have been plotted on Figure 4. The curve shows that the maximum yield available from the hake stock is about 140,000 metric tons per annum and that this could be harvested with about 25,000 units of effort.

F. DISCUSSION

Good documentation of catch and effort data for the Cape of Good Hope hake stock has enabled the yield from this stock to be assessed using three methods. The resulting yield curves have been plotted on Figure 5 to facilitate comparison. It is apparent that all three methods indicate that a yield in the vicinity of 150,000 metric tons per annum is available from the stock with the fishing gear used during the study period, that is up until 1973.

During the period 1964 to 1973 fishing was conducted mainly by Japan, South Africa, Spain and the U.S.S.R. These countries used nets with different mesh sizes, ranging from 70 mm to 120 mm, so that it is difficult to generalise on the effective mesh size of the entire fleet in these years. Mesh selection studies (Anon. 1973) indicated, though, that the adoption by all boats of a minimum mesh size of 110 mm in place of 90 mm could increase the yield by between 5 and 13 per cent. As a result, a 110 mm minimum mesh size was introduced on the 1st July 1975 and this should raise the maximum sustainable yield.

The exact size of the increase in catch in the long term will depend on the proportion of the catch which was landed by different mesh nets prior to the selection studies.

The levels of fishing effort in 1972 and 1973 were 52,600 and 34,500 units respectively, considerably in excess of the 25,000 units that the generalized stock production model and catch-per-unit-effort on effort predictions suggest would be necessary to harvest the maximum sustainable yield. The yield-per-recruit analysis indicates that this maximum yield could be reaped by even less effort, that is 10,000 units.

These results are based upon a period during which recruitment was constant. The apparent increase in the abundance of

three-year-old fish in 1971 and 1972 might be expected to affect the yield in subsequent years as these year classes make a larger contribution to the catch. The validity of the increase in the number of recruits is however in some doubt, as discussed above. Until this problem has been resolved it should be assumed that under normal circumstances the Cape of Good Hope fishing grounds can yield catches of the order of 150,000 metric tons.

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TABLE 1. Catch and effort statistics for hake on the Cape of Good Hope grounds (ICSEAF Division 1.6)

Year(s)	Total catch (Thousands of metric tons)	Catch per unit effort (Thousands of metric tons per standard trawler day)	Total effort (Stan- dard trawler days)	Average total effort of the two previous years. (Standard trawler days)
1940-47	26	14.20	1,831	...
1955	83	12.45	6,667	...
1956	85	11.25	7,556	...
1957	91	11.85	7,679	7,111
1958	94	11.70	8,034	7,618
1959	105	11.70	8,889	7,857
1960	115	12.45	9,237	8,462
1961	107	8.70	12,229	9,063
1962	107	10.20	10,490	10,768
1963	127	10.05	12,637	11,395
1964	123	10.50	11,714	11,564
1965	168	7.80	21,538	12,176
1966	156	7.65	20,392	16,626
1967	146	7.20	20,278	20,965
1968	109	7.20	15,139	20,335
1969	135	6.20	21,774	17,709
1970	124	5.20	23,846	18,457
1971	189	5.10	37,059	22,810
1972	195	4.00	48,750	30,453
1973	178	3.60	49,444	42,904
Average for 1965-69	143	7.21	19,824	...

TABLE 2. The numbers of fish caught from each age-class in the Cape of Good Hope (ICSEAF Division 1.6) hake stock, 1964-1973

Year	Numbers of fish caught (millions)											
	A G E											
	0	1	2	3	4	5	6	7	8	9	10	11
1964	0.9	3.2	6.3	9.6	13.7	11.2	5.5	2.9	1.5	2.0
1965	1.2	3.5	8.0	15.2	19.8	15.7	7.7	3.9	1.9	2.3
1966	16.2	32.4	48.2	30.8	19.3	5.6	1.4	0.5	0.2
1967	22.2	40.4	42.6	23.5	12.6	3.4	0.8	0.6	2.8
1968	0.2	20.6	34.9	34.6	18.5	11.0	3.6	0.8	0.7	0.1
1969	9.6	55.0	56.4	29.3	21.8	12.1	4.2	1.2	0.3	0.0
1970	...	0.5	17.3	54.3	50.6	27.6	18.0	9.7	3.6	1.2	0.4	0.0
1971	...	6.5	66.5	148.0	75.9	25.2	19.1	9.4	4.3	1.3	0.4	0.2
1972	...	10.3	191.0	271.0	141.0	23.1	14.6	6.2	2.5	0.4	0.2	...
1973	156.0	106.0	42.8	13.1	6.9	2.0	0.3	0.3	...

TABLE 3. Fishing mortality estimates for the Cape of Good Hope (ICSEAF Division 1.6) hake stock using different terminal fishing mortalities. (Assumed natural mortality = 0.25)

Terminal Fishing Mortality												
Age	1 9 6 8				1 9 7 0				1 9 7 2			
	1.2	1.7	1.8	Ratio 1.8/1.2	1.2	1.7	1.8	Ratio 1.8/1.2	1.2	1.7	1.8	Ratio 1.8/1.2
3	0.106	0.107	0.107	1.01	0.260	0.272	0.274	1.05	0.471	0.585	0.604	1.28
4	0.312	0.313	0.313	1.00	0.505	0.522	0.524	1.04	0.764	0.900	0.922	1.21
5	0.486	0.488	0.488	1.00	0.519	0.529	0.530	1.02	0.579	0.676	0.691	1.19
6	0.557	0.559	0.559	1.00	0.721	0.726	0.727	1.01	0.774	0.866	0.879	1.14
7	0.828	0.840	0.841	1.02	0.861	0.874	0.875	1.02	1.005	1.112	1.127	1.12
8	0.835	0.853	0.856	1.03	1.025	1.044	1.046	1.02	1.639	1.773	1.792	1.09
9	1.211	1.211	1.211	1.00	1.014	1.122	1.137	1.12	0.539	0.611	0.621	1.15

TABLE 4. Biomass estimates (metric tons $\times 10^{-5}$) for the Cape of Good Hope (ICSEAF Division 1.6) hake stock using different terminal fishing mortalities. (Assumed natural mortality = 0.25)

Terminal Fishing Mortality								
Year	Total Biomass				Biomass of fish aged 4 and older			
	1.2	1.7	1.8	Ratio 1.2/1.8	1.2	1.7	1.8	Ratio 1.2/1.8
1964	5.55	5.50	5.49	1.01	4.13	4.09	4.08	1.01
1965	6.21	6.13	6.12	1.01	4.80	4.73	4.71	1.02
1966	6.06	6.02	6.01	1.01	4.69	4.65	4.65	1.01
1967	5.38	5.33	5.32	1.01	4.12	4.07	4.06	1.01
1968	4.87	4.84	4.83	1.01	3.53	3.51	3.51	1.01
1969	5.28	5.19	5.16	1.01	3.45	3.43	3.43	1.01
1970	5.19	5.04	5.00	1.04	3.03	2.98	2.98	1.02
1971	7.62	6.79	6.73	1.13	2.88	2.77	2.76	1.04
1972	8.13	6.94	6.76	1.20	3.28	2.98	2.94	1.12

TABLE 5. Biomass estimates (metric tons $\times 10^{-5}$) for the Cape of Good Hope (ICSEAF Division 1.6) hake stock using different natural mortalities. (Assumed terminal fishing mortality = 1.7)

Year	Natural Mortality							
	Total Biomass				Biomass of fish aged 4 and older			
	0.10	0.25	0.30	Ratio 0.3/0.1	0.10	0.25	0.30	Ratio 0.3/0.1
1964	3.95	5.50	6.37	1.61	3.14	4.09	4.49	1.43
1965	4.66	6.13	6.86	1.47	3.80	4.73	5.11	1.34
1966	4.69	5.97	6.61	1.41	3.83	4.65	4.99	1.30
1967	4.19	5.33	5.82	1.39	3.34	4.07	4.38	1.31
1968	3.84	4.83	5.27	1.37	2.87	3.51	3.79	1.32
1969	4.07	5.19	5.66	1.39	2.86	3.43	3.66	1.28
1970	4.08	5.03	5.40	1.32	2.51	2.98	3.17	1.26
1971	5.38	6.80	7.19	1.34	2.40	2.77	2.91	1.21
1972	6.01	6.94	7.30	1.21	2.64	2.98	3.10	1.17

TABLE 6. Fishing mortality estimates for the Cape of Good Hope (ICSEAF Division 1.6) hake stock, 1964-1973. (Assumed natural mortality = 0.25 and assumed terminal fishing mortality = 1.7)

Year	A G E											
	0	1	2	3	4	5	6	7	8	9	10	11
1964	0.003	0.016	0.054	0.134	0.351	0.602	0.355	0.740
1965	0.004	0.017	0.055	0.190	0.477	0.952	1.268	0.492	2.184	...
1966	0.078	0.230	0.575	0.773	1.386	1.299	0.893	0.119	1.700
1967	0.125	0.301	0.570	0.667	0.944	1.164	0.669	1.365	1.700
1968	0.001	0.107	0.313	0.488	0.559	0.840	0.853	1.211	3.330	1.700
1969	0.032	0.297	0.503	0.504	0.705	0.986	1.036	0.912	5.000	1.700
1970	...	0.001	0.029	0.272	0.522	0.529	0.726	0.874	1.044	1.122	0.856	1.700
1971	...	0.004	0.081	0.400	0.812	0.577	0.959	1.238	1.505	1.875	1.700	1.700
1972	0.192	0.585	0.900	0.676	0.866	1.112	1.773	0.611	1.700	...
1973	0.250	0.510	0.850	1.190	1.700	1.700	1.700	1.700	...
Average for 1965-69	0.007	0.125	0.280	0.465	0.636	1.018	1.124	0.835	2.400	1.360

TABLE 7. Average fishing mortality (\bar{F}_{7-9}) for fish aged seven to nine, total effort, and catchability coefficient (q) for the Cape of Good Hope (ICSEAF Division 1.6) hake stock, 1964-1972. (Assumed natural mortality = 0.25 and assumed terminal fishing mortality = 1.7)

Year	\bar{F}_{7-9}	Total effort (Standard trawler days)	$q \times 10^{-4}$
1964	0.566	11,714	0.483
1965	0.904	21,538	0.420
1966	1.193	20,392	0.585
1967	0.926	20,278	0.457
1968	0.968	15,139	0.639
1969	0.978	21,774	0.449
1970	1.013	23,846	0.425
1971	1.539	37,059	0.415
1972	1.165	48,750	0.239
Average 1964-72			0.457

TABLE 8. The numbers of fish at age in the Cape of Good Hope (ICSEAF Division 1.6) hake stock, 1964-1973. (Assumed natural mortality = 0.25 and assumed terminal fishing mortality = 1.7)

Numbers of fish (millions)												
Year	A G E											
	0	1	2	3	4	5	6	7	8	9	10	11
1964	451	428	322	227	135	86.2	51.8	27.6	20.8	6.2
1965	484	351	333	236	169	99.1	58.5	28.3	11.8	11.3	2.3	3.1
1966	406	377	274	243	177	123.0	63.6	28.2	8.5	2.6	5.4	0.2
1967	566	317	293	213	175	110.0	53.9	22.8	5.5	1.8	0.8	3.7
1968	1,130	441	247	229	146	100.0	48.1	21.5	6.9	1.3	0.7	0.2
1969	668	878	343	241	160	82.9	47.9	21.4	7.2	2.3	0.3	...
1970	2,370	520	684	256	139	75.0	38.9	18.4	6.2	2.0	0.7	...
1971	307	1,850	965	505	152	64.3	34.4	14.7	6.0	1.7	0.5	0.2
1972	...	239	1,230	684	263	52.4	28.1	10.3	3.3	1.0	0.2	...
1973	791	297	83.1	20.7	9.2	2.6	0.4	0.4	...
Average for 1965-69	651	473	298	232	165	101.0	54.4	24.4	8.0	3.9	1.9	1.4

TABLE 9. Initial guesses and associated limits for parameters used in the generalized stock production model for the Cape of Good Hope (ICSEAF Division 1.6) hake population.

Parameter	Best guess	Lower limit	Upper limit
f_{opt}	18,597.0	1,860.0	185,970.0
r	0.8	0.0	1.0
U_{max}	13.0	1.3	130.0
q	0.00003	0.00003	0.00003

TABLE 10. Coefficients for the Cape of Good Hope (ICSEAF Division 1.6) hake stock as calculated by the generalized stock production model for different choices of l . (Assumed catchability coefficient = 0.00003)

l	H	K	R
0.10	5.6×10^4	0.3	0.88
0.30	6.2×10^3	0.5	0.87
0.50	8.3×10^2	1.2	0.86
0.70	1.2×10^2	2.4	0.84
0.90	3.1×10^1	8.4	0.82
1.10	-2.6×10^0	-9.6	0.79
1.30	-7.5×10^{-2}	-3.6	0.77
1.50	-3.6×10^{-3}	-2.3	0.74
1.70	-2.2×10^{-4}	-1.9	0.72
1.90	-1.5×10^{-5}	-1.7	0.69
2.00	-3.9×10^{-6}	-1.5	0.68

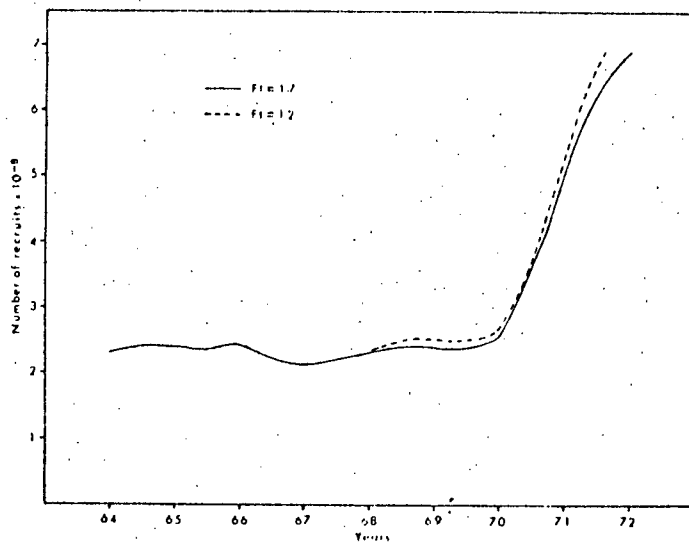


Fig. 1: Number of 3 year-old hake recruits

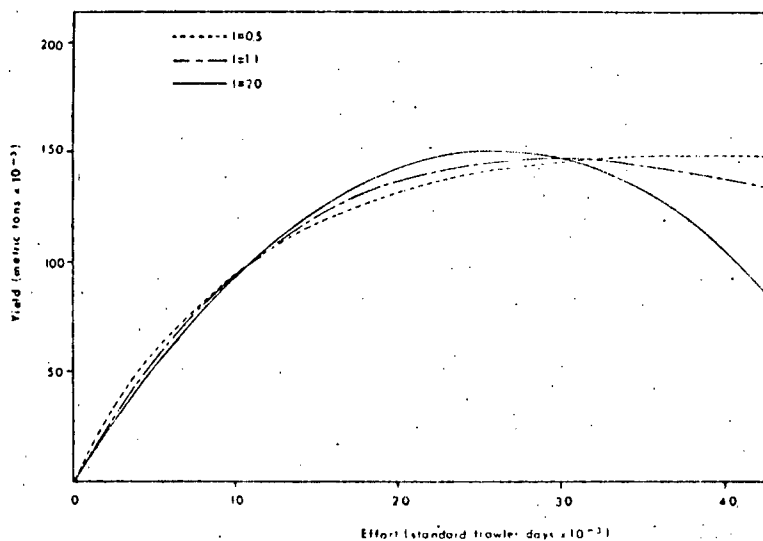


Fig. 2: Stock production yield curves for hake of ICSEAF Div. 1.6

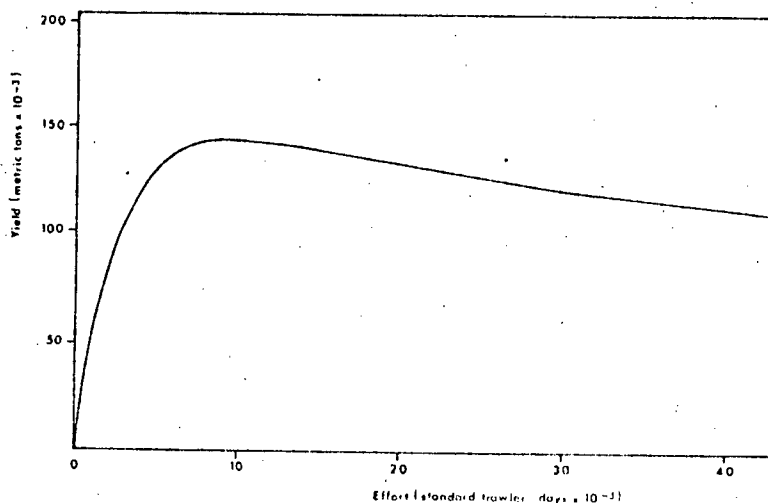


Fig. 3: Yield from recruitment of hake of ICSEAF Div. 1.6

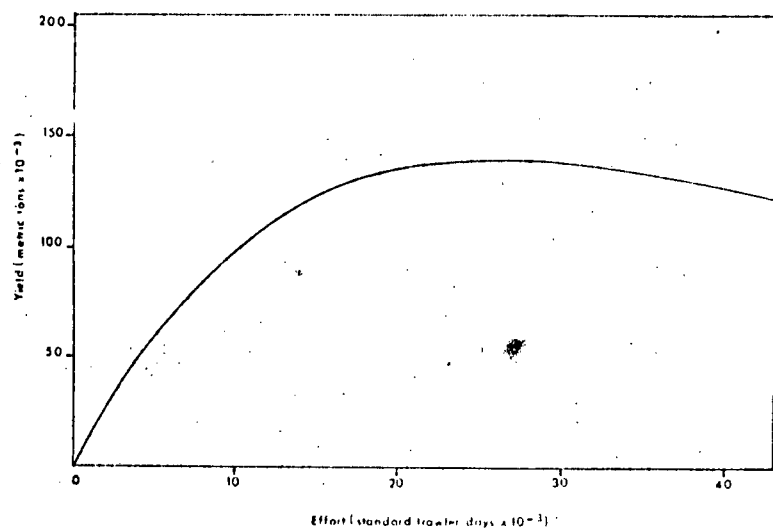


Fig. 4: Yield from catch per unit effort for hake of ICSEAF Div. 1.6

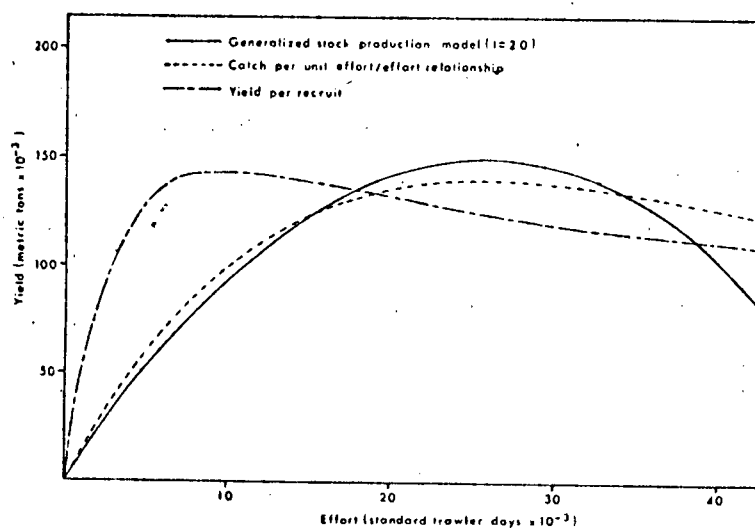


Fig. 5: Comparison of yield curves for hake of ICSEAF Div. 1.6

Distribution of major species in South African pelagic fishery

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SOME 180 000 catch reports, submitted by skippers of purse seine vessels and processing factories of the South African pelagic fishery throughout the period 1964 to 1972, have recently been analysed by the Sea Fisheries Branch. One of the aims of this analysis was to determine the distribution of the catches of the various species, and the results are discussed in this paper.

The fishing grounds were divided into 28 sectors, chosen to show any change in the fishing pattern occurring along the coastline and in an inshore-offshore direction. For each sector the catch per unit area by species over the nine-year period was determined in short tons per square mile, and these yields are mapped in Figs. 1 to 6. The catches over the nine-year period were considered together, as there were few major differences in the fishing patterns during this period. Generally the area having the highest yield for a particular species was the same from year to year, though occasionally there was a shift to adjacent areas. The significant changes that have occurred in the distribution of the catches are discussed below and the annual landings of each species during the period considered are shown in Table I.

The catch in any sector will be influenced by the accessibility of that particular sector to the fishing

fleet. Thus, for example, the catch may be expected to be high in the St. Helena Bay vicinity where large numbers of boats are based. Currently, five factories processing pelagic fish are situated in this bay, between the Berg River mouth and Stompneus Point. A further two are located at Saldanha Bay and one each at Lambert's Bay, Hout Bay and Gans Bay.

That the yield per unit area is, however, a pointer to the actual density distribution of the species is shown by the differing patterns obtained for the six species. Table II compares some of the more important regions, giving an indication of their productivity, as well as showing the percentage of the total landings made from catches west of Cape Point and from catches inside the 100 fm contour.

Anchovy

In recent years the anchovy has been the major contributor to the South African pelagic catch. In 1965 and subsequent years all boats were allowed to carry the small-meshed "anchovy net" ($\frac{1}{2}$ in. stretched mesh). In 1964, however, only limited numbers of boats were permitted to operate with this net, which accounts for the low catch in that year.

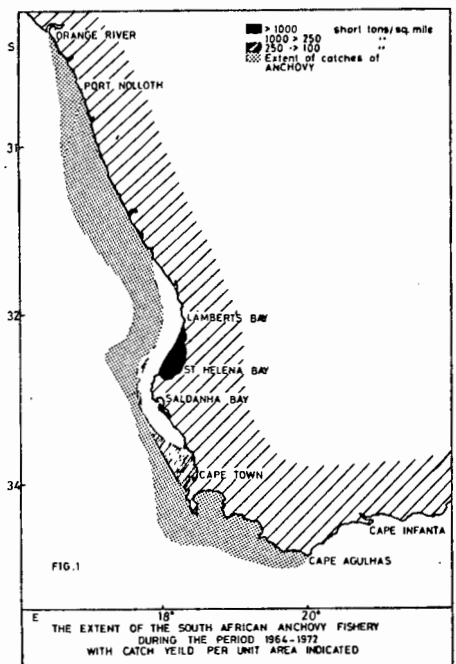
The distribution of the anchovy indicates its greater availability in the cooler waters west of

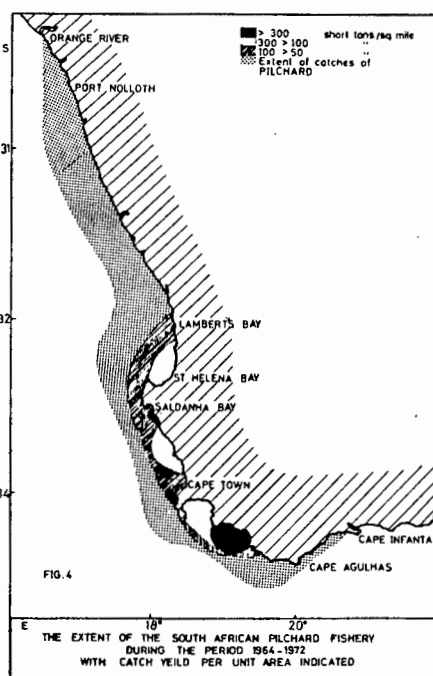
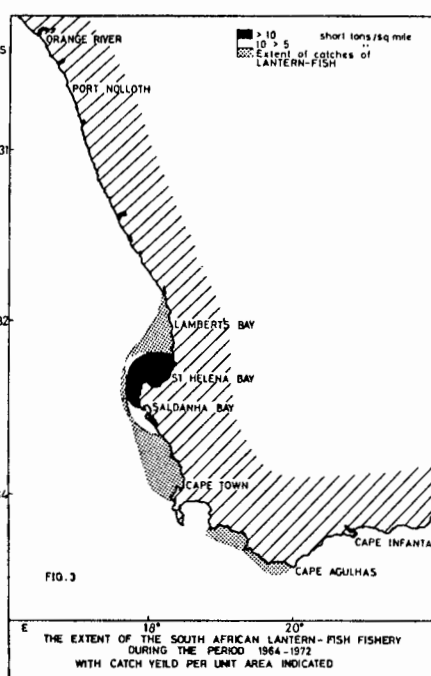
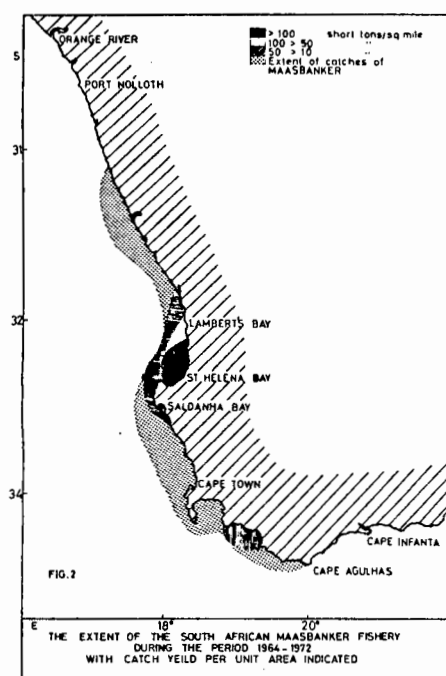
TABLE I. Annual catches in the Western Cape pelagic fishery, 1964-1972 (Thousands of short tons).

Year	Anchovy	Maas-banker	Lantern-fish	Pilchard	Red-eye	Mackerel	Total
1964	102	27	—	282	—	57	468
1965	196	64	—	225	—	45	530
1966	173	30	—	126	5	61	395
1967	304	9	—	81	14	153	561
1968	187	1	—	104	15	99	406
1969	189	28	1	54	14	102	387
1970	237	8	20	45	3	86	399
1971	203	2	3	72	16	60	356
1972	309	1	17	68	22	61	478

TABLE II. Yield per unit area of six South African pelagic species, and percentage of each species caught west of Cape Point and inside the 100 fm contour (1964-1972).

Species	Yield (short tons per sq. mile)			Percentage of total catch	
	St. Helena Bay	Dassen Island - Bok Point	Walker Bay	West of Cape Point	Inside 100 fm contour
Anchovy	1295	183	82	95	99
Maasbanker	114	3	19	91	99
Lantern-fish	17	< 1	< 1	99	100
Pilchard	174	132	348	57	98
Red-eye	5	33	7	84	95
Mackerel	185	236	15	97	84





Cape Point, and especially in areas of strong upwelling with the consequent abundance of plankton (Fig. 1). St. Helena Bay had an especially high yield of anchovy – in excess of 1 000 short tons per square mile for the nine-year period. In this region the northward drift of the Benguela Current, leaving the coastline at Cape Columbine, and an inshore counter current in the Lambert's Bay vicinity, may produce a cyclonic movement of the water in the bay. Water in motion in the southern hemisphere is deflected to the left of its path of travel, according to the Coriolis effect, so that the surface water would move away from the centre of this cyclonic pattern. The result would be upwelling and a mixing of nutrients, a condition favourable for plankton blooms.

Maasbanker

The distribution of maasbanker catches was similar to the pattern obtained for anchovy, although catches did not extend north of 31°S or as far offshore (Fig. 2). Again, St. Helena Bay was the most productive area, but catches of this species have declined since the 1950's when, together with the pilchard, it formed the basis of the fishery. Throughout the years considered, only during 1964-1966 and in 1969 did the catch exceed 10 000 short tons.

Lantern-fish

The lantern-fish was most heavily exploited in an area including St. Helena Bay and the Cape Columbine vicinity (Fig. 3). At present it has the most restricted range of the commercially fished pelagic species, 84 per cent of the catch being made in this area. Lantern-fish made their first documented appearance in the commercial catches in 1966 but it was not until 1969 that their catch weight was recorded separately from the anchovy (Centurier-Harris 1974).

Pilchard

Pilchard catches extended from the Orange River beyond Cape Agulhas toward Cape Infanta (Fig. 4). Lesser quantities were also landed on the Natal coast during the "sardine runs." These, however, have not

been included in the annual catches, or in the yield, per unit area.

The fishing grounds between Cape Hangklip and Danger Point were those most heavily exploited for the pilchard. Baird (in press) has shown that since 1966 the catches of adult pilchard have been confined to the waters east of Cape Point. During the nine-year period, however, the yield per unit area was also high in the Dassen Island – Bok Point vicinity and in St. Helena Bay.

The bulk of the catch near the Orange River mouth was made in 1965 and 1966. This area also yielded small amounts of pilchard in 1964 and 1971, but not in any other year. Most of the pilchard from the grounds east of Cape Point is landed between January and March. In recent years the catch has declined.

Red-eye

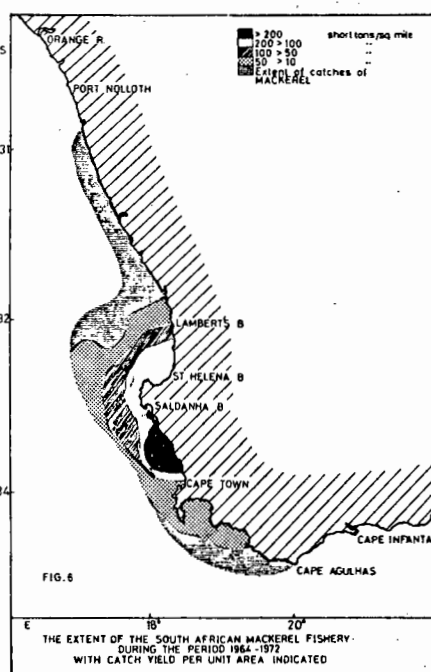
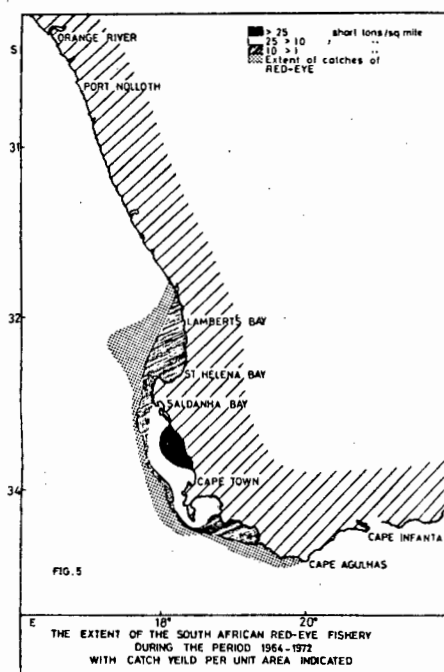
Sixty-five per cent of all the red-eye landed was caught in the inshore region between North Head at Saldanha Bay and Cape Point, but mostly in the region of Dassen Island and Bok Point (Fig. 5). In 1966 there was a significant contribution from the grounds to the north of Saldanha Bay.

Mackerel

Mackerel catches were also heaviest in the Dassen Island-Bok Point vicinity (Fig. 6). It differs from the other species in that a significant proportion of the catch was pursued outside the 100 fm contour (Table II).

Most of this catch was netted in the sector west to northwest of Cape Columbine, the area from which the late autumn or winter run of large mackerel is initiated. These catches were first made in 1968. From the offshore waters, the large mackerel move toward Cape Columbine and then turn southward, increasing catches in the Dassen Island vicinity.

It is interesting to note that the Cape Columbine region is that where the lantern-fish are most abundant. This species has been shown to form an



important part in the diet of the large mackerel (Baird 1974).

Discussion

The heavy yield of all species from the cool in-shore waters west of Cape Point may be attributed to the abundant supply of food-plankton found in these waters, which results from the upwelling mentioned above. Large mackerel are also caught in waters further offshore. On account of their piscivorous habits they are not as dependent on this supply of food-plankton as are the smaller mackerel and the other pelagic species.

The large yield of pilchard east of Cape Point is in marked contrast to the lower yields of other species in this region and it is interesting to note the parallel in the developments of the South African pelagic fishery and that of California. Murphy (1966), in describing the collapse of the fishery based on the Pacific sardine, considered two components of this sardine stock, a northern one and a southern one. The northern fishery disappeared completely after 1948, and this was followed by a progressive southward shift in the site of most landings until the fishery was centred off Baja California. Thus the decline of the sardine was characterised by a progressive decrease in range as well as numbers. Moreover, the range contracted to the warmer waters of the south, and this was

accompanied by an increase in the population of the anchovy in the cooler waters at the north of the fishery. Murphy considered the rise in the anchovy population to be a response to the environmental void created by the decline of the sardine.

Prior to the decline in the stocks of the South African pilchard, large yields of pilchard were obtained from the cooler waters west of Cape Point (Stander and Le Roux 1968). At present, the yield is highest in the warmer waters to the east, and there is a high yield of anchovy on the west coast. However, it is not certain that the rise of the South African anchovy population can be attributed to an environmental void created by the decline of the pilchard (Newman et al in press).

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APPENDIX 3

BIOMASS ESTIMATES OF SOME PELAGIC SPECIES IN SOUTH AFRICA (metric tons x 10³)

YEAR	PILCHARD ¹	MAASBANKER ²	MACKEREL ²	RED-EYE ¹	ANCHOVY ³	TOTAL
1950	910	625				1 535
1951	926	700				1 626
1952	860	679				1 539
1953	712	620				1 332
1954	637	560				1 197
1955	736	456				1 192
1956	1 040	409				1 449
1957	1 520	437				1 957
1958	1 890	461				2 351
1959	2 040	541				2 581
1960	1 940	632				2 572
1961	1 700	654				2 354
1962	1 370	661				2 031
1963	989					989
1964	598		83	215	306	1 202
1965	382		60	345	306	1 093
1966	243		144	484	289	1 160
1967	259		251	577	343	1 430
1968	286		201	521	246	1 254
1969	241		160	473	287	1 161
1970	235		108	623	326	1 292
1971	254		89	573	295	1 211
1972	189		103	498	290	1 080
1973	203		101	432	370	1 106
1974	350		84	253	384	1 071
1975	550				332	882
1976	529				309	838

1 Natural mortality = 0,50

2 Natural mortality = 0,25

3 Natural mortality = 0,80